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Vertical Connectivity Influences Secondary Production, Community Diversity, and Resilience in an Ozark Stream

Nathan C. Dorff
Missouri State University, Dorff104@live.missouristate.edu

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VERTICAL CONNECTIVITY INFLUENCES SECONDARY PRODUCTION, COMMUNITY DIVERSITY, AND RESILIENCE IN AN OZARK STREAM

A Master's Thesis
Presented to
The Graduate College of
Missouri State University

In Partial Fulfillment
Of the Requirements for the Degree
Master of Science, Biology

By
Nathan C. Dorff
May 2019

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Biology

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Master of Science

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ABSTRACT

The hyporheic zone, a key component of stream vertical connectivity, supports stream function (e.g., nutrient regeneration) and provides habitat for aquatic biota. The Ozark Highlands ecoregion contains gravel-bed streams that have extensive hyporheic zones and that are subject to recurrent flash floods. I sampled *Leuctra tenuis* (Pictet) nymphs from the hyporheic habitat (30-45 cm below the streambed) in a gravel-bed reach and an intermittent tributary of an Ozark stream from early instar to adult emergence. Concurrently, I sampled benthic insects in two reaches of the same stream that differed primarily in amount of hyporheic habitat (bedrock vs. gravel) and monitored the hyporheic insect community in the gravel reach for an entire year (October 2017 to September 2018). I calculated secondary production and development of hyporheic *L. tenuis*. I also monitored the response of benthic and hyporheic insect communities after two floods and documented reductions in richness and densities of benthic insects, especially in the bedrock reach. Pre- and post-flood communities were significantly different between bedrock and gravel benthic habitats. However, differences in community composition were not significant across the entire year, indicating that floods mixed the communities. Insect richness in the hyporheic zone increased post-flood, which may have facilitated quicker recovery in the gravel reach. It is imperative that we understand the role of vertical connectivity to stream secondary production and how the hyporheic zone can contribute to supporting diverse and resilient aquatic communities in order to better protect stream ecosystems.

KEYWORDS: interstitial, flow, gravel-bed, diversity, resilience, hyporheos, life-history, ephemeral

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Approved:

Debra Finn, Ph.D., Thesis Committee Chair

Sean P. Maher, Ph.D., Committee Member

David E. Bowles, Ph.D., Committee Member

Julie Masterson, Ph.D., Dean of the Graduate College

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OVERVIEW

Streams are dynamic ecosystems that vary through space and time. Stream ecosystem function relies on connectivity in three spatial dimensions: longitudinal (upstream-downstream), lateral (stream-floodplain), and vertical (surface-subsurface). Foundational research has emphasized longitudinal (Hynes, 1975; Vannote et al., 1980) and lateral connectivity (Junk et al., 1989), whilst vertical connectivity remains understudied (Gibert et al., 1990; Boulton, 2007). An important aspect of vertical connectivity is the hyporheic zone, a habitat below the streambed that spreads laterally from the main channel and where exchanges between surface and groundwater occur (Fig 1). The hyporheic zone provides unique habitat and a potential refuge from extreme flow events for aquatic macroinvertebrates (Stanford & Ward, 1993; Boulton et al., 1998) and it contributes substantially to stream ecosystem function (e.g., nutrient transformation and secondary production, Boulton et al. 1998).

Macroinvertebrates are ubiquitous, diverse, and well-studied from benthic habitats in stream systems (Merritt et al., 2008). Less is known about which macroinvertebrates occupy the hyporheic zone and how they use this unique habitat (Boulton, 2007). Some macroinvertebrates have obligate or permanent stages within the hyporheic zone, remaining in the hyporheic zone for part or all of their development (Stanford & Gaufin, 1974; Stanford & Ward, 1993), while other macroinvertebrates use the hyporheic zone temporarily as a refuge from flooding and drying events (Dole-Olivier et al., 1997; Wood et al., 2010; Vadher et al., 2017). By contributing unique taxa (obligate inhabitants) and protection for other taxa (facultative inhabitants), the hyporheic zone can boost overall stream diversity in habitats where vertical connectivity is strong (Fig 2; Ward et al. 1998). The hyporheos, or the fauna that occupy the hyporheic zone, has been studied throughout the world (see Boulton et al. 2010 for review). However, only a few studies of the hyporheos have been conducted in the Ozark Highlands ecoregion (Hunt & Stanley, 2003; Distefano et al., 2009), a region containing streams with deep gravel-beds that create extensive hyporheic zones.

Macroinvertebrates often account for a significant amount of biomass production within streams (Benke, 1984; Benke & Huryn, 2017). Annual secondary production of macroinvertebrates, especially insects, has been estimated from streams across the world (see Benke and Huryn 2010 for review) and has garnered significant attention for its importance to broader food webs, both aquatic and terrestrial (Jackson & Fisher, 1986; Nakano & Murakami, 2001; Benke & Huryn, 2010). Annual production rates vary substantially, ranging from 10 to >500g DM m^{-2} yr^{-1} (Huryn & Wallace, 2000). Some estimates for production within the hyporheic zone have also been calculated and can be a substantial portion of overall stream production (up to 20%; Smock et al. 1992, Huryn 1996). Additionally, certain taxa of invertebrates have been shown to have higher rates of production in the hyporheic habitats compared to benthic habitats in the same streams (Collier et al., 2004; Wright-Stow et al., 2006; Reynolds & Benke, 2012). Still, no known attempts have been made to estimate secondary production of hyporheic invertebrates in Ozark streams.

The Ozark Highlands ecoregion (Ozarks) is dominated by karst topography and contains streams with deep gravel-beds that create extensive hyporheic zones. Ozark streams also alternate between gravel-bed reaches with substantial (>2 m deep) vertical connectivity and bedrock-lined reaches where vertical connectivity is limited (<10 cm). In the Ozarks, stream reaches that vary in extent of vertical connectivity can be merely meters apart, creating a natural system in which to study the influence of hyporheic habitat on stream processes. Some Ozark streams are also flashy (Leasure et al., 2016) and despite being groundwater fed, rise rapidly in response to heavy rainfall events. The flashiness combined with considerable vertical connectivity make stream systems in the Ozarks ideal for testing whether macroinvertebrates use the hyporheic zone as a refugium from extreme flow events and whether vertical connectivity can help support diverse and resilient aquatic communities.

My study set out to investigate whether vertical connectivity could influence stream secondary production, community diversity, and community resilience in the face of disturbance in an Ozark stream with minimal anthropogenic impact. The first chapter focused on the life-history and secondary production rates of a stonefly species whose nymphs developed in the hyporheic zone. I calculated secondary production and compared development rates of stonefly nymphs between two thermally distinct hyporheic habitats. The second chapter evaluated the role of vertical connectivity in supporting benthic insect community diversity and resilience and examined some of the spatial and temporal patterns that were observed.

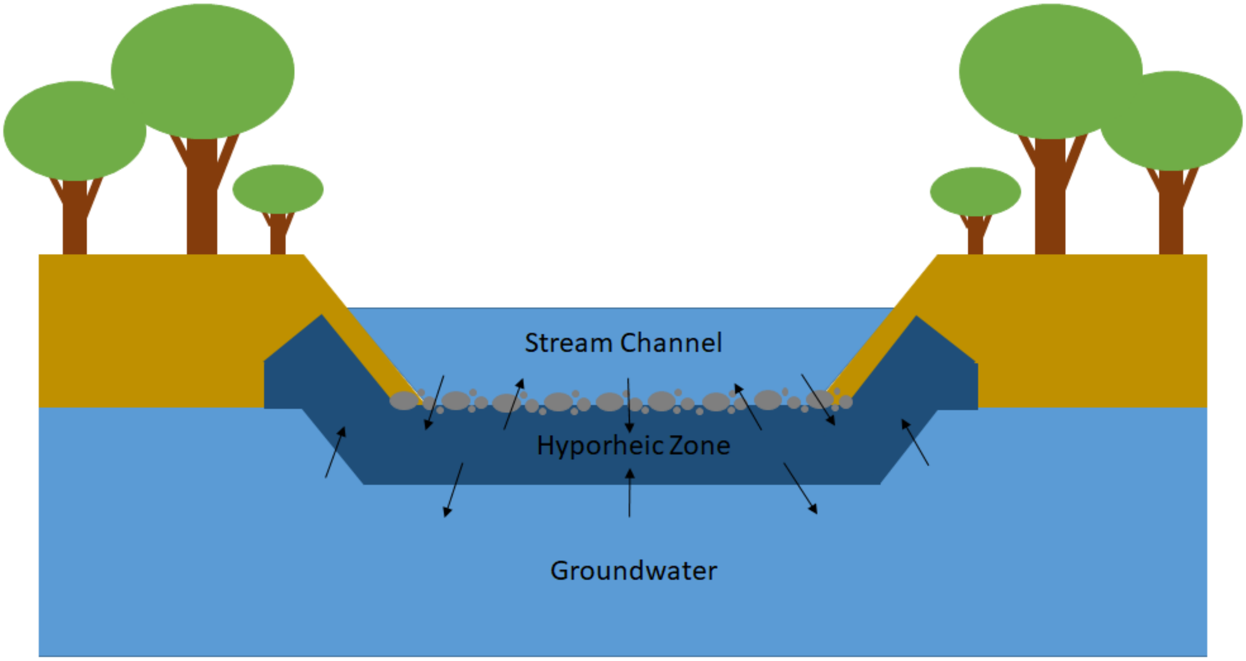

Figure 1. Diagram illustrating stream and groundwater exchange in the hyporheic zone (arrows) and the lateral extension of the hyporheic zone.

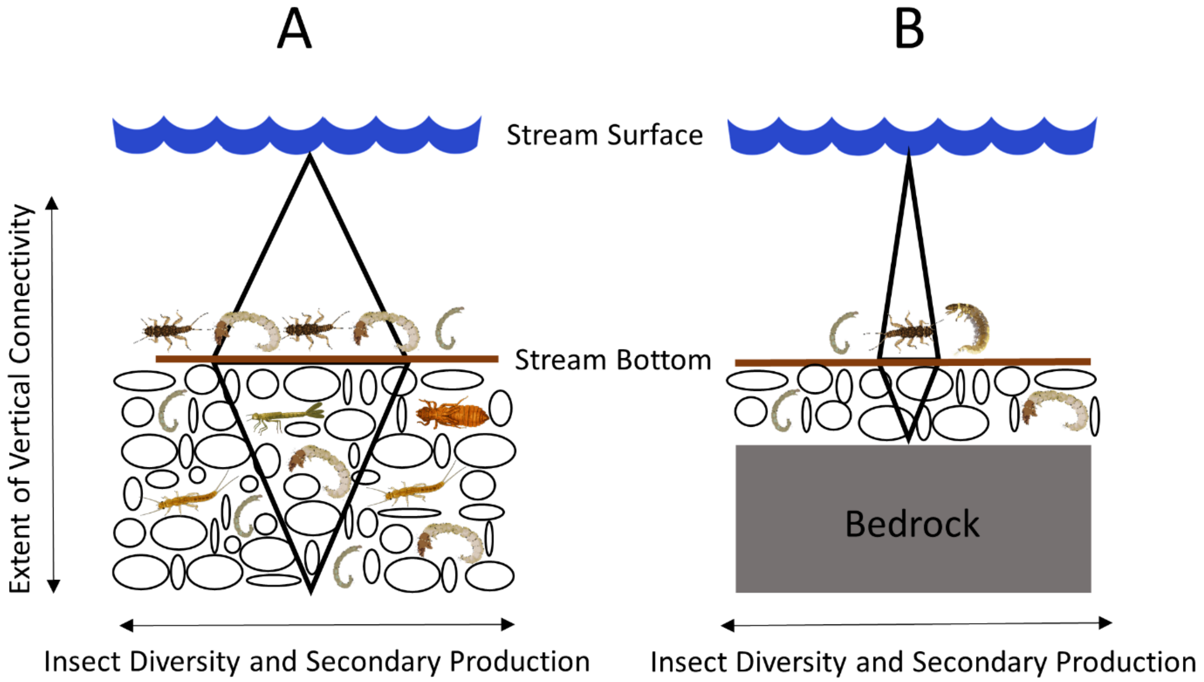

Figure 2. Gravel-bed reach (A), showing increased diversity and secondary production (aquatic insect biomass). Bedrock-lined reach (B) showing decreased vertical connectivity, which decreases diversity and secondary production. Modified from Ward et al., 1998.

HYPORHEIC SECONDARY PRODUCTION AND LIFE-HISTORY OF A COMMON OZARK STONEFLY

Introduction

Secondary production provides information on how much chemical energy is available for higher trophic levels in food webs (Benke, 1993). In lotic ecosystems, macroinvertebrates are often the dominant source of consumer biomass and thus contribute substantially to stream secondary production (Benke, 1984). Secondary production in aquatic ecosystems has been well studied and its importance appreciated especially from areal studies of the benthos (see Benke & Huryn, 2010 for a review) and other habitats within the water column (e.g., snags, Benke et al., 1985). However, little is known about secondary production in hyporheic zones. The hyporheic secondary production studies that do exist have found that only looking at the top 5–10 cm of streambed, the common approach in benthic studies, could result in underestimations of whole-stream secondary production by up to 20% (Smock et al., 1992; Huryn, 1996). Others have estimated secondary production of specific taxa or groups of taxa and have shown that hyporheic habitats are important at a population level, with habitats at depths >10 cm below the streambed contributing >76% of total secondary production for several taxa (Collier et al., 2004; Wright-Stow et al., 2006; Reynolds & Benke, 2012).

Stoneflies (Insecta: Plecoptera) are an ecologically important group of aquatic macroinvertebrates that often are water quality indicators and can make up a significant proportion of overall stream secondary production (Stewart & Stark, 2002). Some families of stoneflies (e.g., Chloroperlidae, Capniidae, and Leuctridae) are either obligate or facultative occupants of the hyporheic zone. For example, Stanford and Gaufin (1974) found nymphs from two stonefly families (Chloroperlidae and Capniidae) that developed entirely in the deep (>4 meters) hyporheic zone of an alluvial river in Montana. In a study from a Mediterranean stream, leuctrid nymphs were found in the benthos only when mature and were shown to spend most of their life cycle in the hyporheic zone (Puig et al., 1990). Therefore, standard methods likely underestimate secondary production because many stoneflies occupy the often unsampled hyporheic zone. Indeed, no known studies have quantified secondary production of stoneflies in the hyporheic zone.

Life history information and secondary production rates of hyporheic stoneflies can help confirm their need for interstitial habitat and their potential to contribute substantial amounts of biomass to the greater food web. The Ozark Highlands ecoregion (Ozarks) in the south-central USA is an ideal location to study production of hyporheic stoneflies. The Ozarks are dominated by karst topography, containing streams with extensive gravel-beds and complex hyporheic zones (Hunt & Stanley, 2003). The Ozarks also has an extensive stonefly fauna, some of which have been proposed to be hyporheic inhabitants because adults are collected in greater abundance than nymphs or in some cases nymphs have never been matched with collected adults (Poulton & Stewart, 1991; Sheldon & Warren, 2009, Andy Sheldon, personal communication). However, I know of no studies from the Ozarks that have confirmed the presence of stonefly nymphs in the hyporheos. Additionally, few studies have looked into the hyporheos of the Ozarks (Hunt, 1999; Distefano et al., 2009) and I know of no studies that have measured hyporheic secondary production rates for any consumer taxa in the Ozarks.

In this study, I measured the secondary production of a hyporheic population of a common stonefly (Plecoptera: Leuctridae) *Leuctra tenuis* (Pictet, 1841) in a second order gravel-bed stream in the Ozarks. I also studied life history characteristics and compared development rates of hyporheic populations of *L. tenuis* between a mainstem reach with perennial surface flow and a small tributary with ephemeral surface flow but perennial, spring-fed hyporheic flow. I predicted that development rates would be slower for the *L. tenuis* population in the ephemeral tributary due to a more constant and relatively cool thermal environment.

Materials and Methods

I studied Bull Creek in the Ozark Highlands ecoregion of southwest Missouri. Bull Creek is designated as an outstanding state resource water (MO DNR, 10 CSR 20-7) and its headwaters are located in a minimally impacted watershed largely comprised of the Mark Twain National Forest. Bull Creek originates on the south side of the Springfield plateau at approximately 420 m elevation and flows southwest through Christian and Taney Counties before emptying into Lake Taneycomo on the White River at approximately 213 m elevation.

Many of the Bull Creek tributaries are ephemeral or intermittent making Bull Creek at the sample reach (hereafter Bull Creek) a second order stream (Fig. 3). The mean annual discharge of Bull Creek at the nearest (approximately 25 km downstream) United States Geological Survey (USGS) gauging station (ID: 07053810) is 6.41 m^3/s and the mean annual discharge of Bull Creek at the study site is 1.32 m^3/s (corrected from USGS gauge data using a factor provided by Claudio Meier, personal communication). An ephemeral tributary (Peckout Hollow), near the Bull Creek sample site contains a deep gravel bed. Although surface flow is ephemeral, a spring located 600 m upstream of the confluence with Bull Creek maintains perennial hyporheic flow in this stretch.

I sampled the hyporheic zone of Bull Creek and Peckout Hollow each month from October 2017 to September 2018 using wells driven to a depth of 45 cm and a Bou-Rouch pump

(Bou & Rouch, 1967). I added two opportunistic sampling dates: one in early March following a flood event and one in late September to follow the life cycle through to mature nymphs. I constructed hyporheic wells from polyvinyl chloride (PVC) pipe (SCH40, ID: 2.5 cm) and created a 15 cm screen in the closed end composed of approximately 45 perforations (5 mm diameter). In Bull Creek, I installed three wells in a medial gravel bar, three upstream of the gravel bar, and three downstream of the gravel bar. I also placed three wells in Peckout Hollow within 30 m of the confluence with Bull Creek. I also installed one well each in Bull Creek and in Peckout Hollow containing a Levelogger® (Model 3001, Solinst®) to record hyporheic water temperature every hour during the sampling period. Leveloggers were not deployed until the first sampling date in 2018 (20 January), so I began calculating degree days from this mid-winter date.

During each sampling event, I pumped 8 L of hyporheic water at a constant rate of approximately 16 liters per minute (Hunt & Stanley, 2000). I filtered the collected hyporheic water using a 250 µm sieve to remove invertebrates. Wells were capped between sampling dates to prevent any outside materials from entering. I stored samples in 95% ethanol in the field and brought them back to the lab for processing. In the lab, samples were sorted using a dissecting microscope to remove *L. tenuis* nymphs. Several of the earlier instars of *L. tenuis* were barcoded using cytochrome oxidase subunit 1 (COI) for species-level confirmation by Barcode of Life Data System (Ratnasingham & Hebert, 2007).

At each sampling event, I also deployed floating emergence traps for 24 hours in order to capture adult aquatic insects. Traps followed the design of Cadmus et al. (2016) with minor modifications. I deployed a total of 12 traps in Bull Creek: four directly on the gravel bar, four upstream, and four downstream. I also deployed four traps directly on dry gravel in Peckout

Hollow. Insects were trapped and stored temporarily in 70% ethanol until they were brought back to the lab and transferred to 95% ethanol within 10 days. I identified *L. tenuis* adults to species level according to Poulton & Stewart (1991). I collected *L. tenuis* nymphs from the benthic zone of Bull Creek using Surber samples as part of a concurrent study in order to compare body lengths with the hyporheic nymphs.

I measured body length from the anterior margin of the labrum to the posterior margin of last abdominal segment of all nymphs of *L. tenuis* to the nearest 0.1 mm using a calibrated ocular micrometer. Dry mass of individuals was estimated using a length mass regression for *L. tenuis* (Benke et al. 1999). I estimated daily and annual hyporheic secondary production of the mainstem *L. tenuis* population using the cohort production method (Benke, 1984; Benke & Huryn, 2017). Total biomass for each sampling event was calculated by multiplying density by mean individual mass. Interval growth was calculated as the change of mean individual mass between sampling dates. I calculated interval production by multiplying mean density of two consecutive sampling dates by mean individual growth. Daily production was calculated by dividing interval production by the number of days between two consecutive sampling dates. Finally, annual secondary production was calculated by adding the sum of the interval production values to the initial biomass. I calculated cohort and annual biomass as the mean biomass across 8 months (the time span between earliest detected instars and adult emergence) and 12 months, respectively. Cohort and annual P/B ratios were calculated by dividing total annual secondary production by cohort and annual biomass respectively. All biomass and secondary production parameters were calculated using R v3.3.3 (R Core Team, 2017).

Earliest instars are typically underrepresented due to low detectability in samples and short duration of time spent in these stages (Benke & Wallace, 1980), which can lead to underestimates of densities. To estimate densities for earliest instars of *L. tenuis*, I fitted a logarithmic curve to mean length versus density and used the following equation to predict densities of the earliest instars (Perán et al., 1999; Studholme et al., 2017):

$$D = a * \ln(L) + b$$

where D is density (numbers of individuals per square meter), L is the mean individual length of individuals from a single sampling date (mm), and a and b are constants. I then used the density estimate to calculate secondary production parameters for the earliest instar of the study cohort as described above.

Because I wanted to compare *L. tenuis* secondary production collected from a volume of hyporheic water to previous studies of *Leuctra* spp. based on areal benthic sampling, I calculated the approximate streambed area below which the volumetric hyporheic samples were collected. To accomplish this, I assumed that pump samples were collected from a cylindrical volume with a height of 15 cm (the length of the screen of my wells). In the field, I filled a container with three volumes (4, 8, and 16 L) of saturated gravel and measured how much water it took to fill the interstitial space. With four replicates at each volume I fit a regression (r^2=0.97) between gravel volume and water volume that allowed me to estimate the volume of gravel that 8 L of water would fill. I calculated a surface area using this regression and determined that a 15 cm tall cylinder that contained 28 L of gravel would contain the 8 L of sampled water. This volume of gravel corresponded to approximately 0.18 m^2 of streambed surface area. Using this surface area estimate generates conservative estimates of densities because it does not take into account the full extent of the vertical dimension of the hyporheic zone.

Results

In Bull Creek, hyporheic temperatures ranged from 4.1˚C to 26.5˚C during the sampling period, whereas hyporheic temperatures ranged between 8.0˚C and 22.7˚C in Peckout Hollow (Fig. 4). Mean daily temperatures in Peckout Hollow were warmer in the winter and cooler in the spring and summer, compared to hyporheic temperatures in Bull Creek. Approximately 3,900 degree days accumulated over 238 days from 20 Jan 2018 until first detection of *L. tenuis* adults in the mainstem of Bull Creek. In Peckout Hollow, it took an additional 18 days to accumulate the same number of degree days (Fig. 5). Although I did not collect adults of *L. tenuis* in Peckout Hollow during the study period, mature nymphs were present on the final sampling date (28 September 2018). These mature nymphs were similar in size and appearance to those found in the hyporheic zone of Bull Creek on 15 September 2018. The lack of emergent adults and the presence of the mature nymphs on 28 September in Peckout Hollow indicates that development took at least 13 days (15 to 28 September) longer than in Bull Creek.

Density of *L. tenuis* peaked in the hyporheic zone of Bull Creek in February at approximately 170 individuals per square meter of streambed and mean individual mass was greatest (0.40 mg) in September (Fig. 6). Nymphs of *L. tenuis* did not appear in benthic samples until April, and mean lengths of hyporheic individuals were significantly different from those in benthic samples from May to July (Welch’s t-test, $P < 0.02$), but in August and September lengths were not significantly different to those in the hyporheic samples (Fig. 7). I detected nymphs of *L. tenuis* in the hyporheic zone throughout development in both Bull Creek and Peckout Hollow. I captured several adults emerging directly through the hyporheic wells (which seemed to facilitate emergence) and from emergence traps deployed on the medial gravel bar. I also captured adults in floating emergence traps on the mainstem of Bull Creek. Adults were present in Bull Creek in September, but adults were not collected in Peckout Hollow before the end of the sampling period (28 September 2018).

In Bull Creek, mean individual mass increased from 0.016 mg in February to 0.40 mg in September (Table 1). Daily production reached a maximum of 0.25 mg m^{-2} d^{-1} between May and June sampling dates. Annual secondary production of *L. tenuis* in the hyporheic zone per unit area streambed was 18.87 mg m^{-2} yr^{-1} or per unit volume was 126 mg m^{-3} yr^{-1}. Cohort and annual biomass were 5.23 and 3.92 mg m^{-2}, respectively. Cohort and annual P/B were 3.61 and 4.82, respectively. Sample sizes of *L. tenuis* from Peckout Hollow were too small to generate an accurate estimate of hyporheic secondary production in the ephemeral tributary.

Discussion

Researchers suspected stonefly nymphs of occupying the hyporheic zone as early as the 1950s and confirmed that nymphs could be found deep within the stream substrate in the 1960s (Williams, 1984). Stanford & Gaufin (1974) found several stoneflies that developed entirely in the hyporheic zone in the Flathead River, Montana. After capturing adults of one leuctrid species in a stream in Colorado, DeWalt & Stewart (1995) noted that nymphs were never found in benthic samples and suggested a possible hyporheic existence. In the present study, *L. tenuis* appears adapted to spend its entire nymphal development in the hyporheic zone and the presence of adults in my hyporheic wells suggests that molting of the final nymphal instar also occurs in the hyporheic zone. To my knowledge, this is the first confirmation of stonefly development in the hyporheic zone from the Ozark Highlands ecoregion.

My hyporheic secondary production estimate is in the range of several estimates of exclusively benthic estimates of secondary production of other *Leuctra* species (Table 2). A few studies have generated substantially greater estimates of hyporheic secondary production for other insect species and illustrate the potential productivity of hyporheic zones (Table 2). Although my estimated annual secondary production of hyporheic *L. tenuis* is a relatively small number, the contribution to the overall population is likely substantial. For instance, Jop & Stewart (1987) found that benthic secondary production of *L. tenuis* in an Oklahoma Ozark stream was 33 mg m^{-2} yr^{-1}. The authors further suggested that they might be underestimating production of several stoneflies due the likelihood that the nymphs were using the hyporheic zone (unsampled in their study). If I compare my estimate with their study in the same ecoregion, they might have underestimated production of *L. tenuis* by up to 32%. Another way to view my estimate of *L. tenuis* production is that approximately 47 adult stoneflies are produced per m^2 of streambed yearly from the shallow hyporheic zone. Furthermore, this estimate includes not just streambed habitat with permanent surface flow, but all hyporheic habitat within the stream channel.

My own estimates of hyporheic secondary production, density, and biomass of *L. tenuis* are likely underestimates because I sampled only a 15 cm vertical stratum of the hyporheic zone. I detected *L. tenuis* nymphs in the benthic zone, but only later instars. Nymphs therefore migrate up into the benthic zone and likely also occur deeper than my sample method was capable of detecting (Stanford & Gaufin, 1974; Williams & Hynes, 1974; Stubbington et al., 2011). Because I found substantial densities of *L. tenuis* in the shallow hyporheic zone from areas both with and without surface flow, I also know that *L. tenuis* is occupying habitat (e.g., medial gravel bar or ephemeral channels) that is not accounted for in standard studies of secondary production that rely solely on benthic collections.

The present study considered a single insect taxon within the hyporheic zone. I also detected several other unreported taxa consistently in the hyporheic zone including non-insect invertebrates (e.g., crustacean meiofauna), and therefore suggest that hyporheic community-level secondary production is likely substantial. To my knowledge, only two studies have attempted to quantify community-level secondary production in the hyporheic zone (Smock et al., 1992; Huryn, 1996). In one of the two streams that Smock et al. (1992) sampled, the hyporheic zone contributed 21% of whole-stream (including floodplain) production. In the stream channel itself, the hyporheic zone accounted for 65% of macroinvertebrate secondary production. Meiofauna (particularly Copepoda and Isopoda) are often diverse and abundant in the hyporheic zone (Pennak & Ward, 1986; Hakenkamp & Palmer, 2000; Hancock et al., 2005; Boulton, 2007) and are probably another significant source of secondary production. Although meiofauna are small from the perspective of individual biomass, their high densities and high P/B can lead to significant contributions to stream secondary production (Stead et al., 2005). More studies on community-level contribution to overall stream secondary production are needed.

Development of *L. tenuis* was strongly predicted by degree-day accumulation as is common in ectotherms (Vannote & Sweeney, 1980; Sweeney & Vannote, 1986). Temperature dependence of cohort development is consistent with a lab study of *L. nigra,* which demonstrated highly predictable increases in growth rates and decreases in development times at higher temperatures (Elliott, 1987). Bottová et al. (2013) found that in a stream with almost constant temperature, photoperiod was positively correlated with growth rate for *L. prima* in a stream in Slovakia. For the present study, dependence on photoperiod is unlikely because negligible amounts of light penetrate the hyporheic zone and thus I have strong evidence that *L. tenuis* is responding directly to temperature. It is not surprising that emergence timing in temperate-zone aquatic insects is strongly correlated to temperature (Harper & Peckarsky, 2006; Finn & Poff, 2008; Sweeney et al., 2018), but it is informative to note the strong influence of temperature in the absence of photoperiod cues. Other abiotic factors (e.g., DO and pH) might influence the development rates of *L. tenuis* and may vary between the main channel and the ephemeral tributary. Dissolved oxygen in particular has been shown to be a limiting factor in the hyporheic zone and warrants further investigation (Boulton et al., 1997; Franken et al., 2001).

Many Ozark streams including Bull Creek have flashy flow regimes due to shallow bedrock (Leasure et al., 2016) and experience flow extremes in both directions (floods and drought). The presence of *L. tenuis* and other benthic taxa in the hyporheic zone is an indication that this habitat may be used as a flow refuge (Dole-Olivier, 2011; Vadher et al., 2017). As a refugium, the hyporheic zone may also act as a point of benthic macroinvertebrate recolonization following disturbance (Hancock, 2002; Vander Vorste et al., 2016). The Ozarks is an underappreciated hotspot for biodiversity, including fish and other vertebrates (Mayden, 1985; Allen, 1990; Robinson & Allen, 1995; Zollner et al., 2005; Skvarla et al., 2015). Invertebrate production provides energy to these higher consumers both in the stream and in adjacent terrestrial systems (Nakano & Murakami, 2001). The results of my study, the first to address the contribution of the hyporheic zone to invertebrate secondary production in the Ozarks, suggests that this habitat plays a major role in the broader stream and riparian food web.

Conclusion

The present study represents the first documentation from the Ozarks of life-history and secondary production for a lotic invertebrate in the hyporheic zone. Cohort development of *L. tenuis* was dependent on degree day accumulation rate. Production of *L. tenuis* in the hyporheic zone of Bull Creek was 18.87 mg m^{-2} yr^{-1}. Hyporheic zones can contribute to overall stream secondary production and neglecting potentially vast hyporheic habitats could result in severe underestimates of biomass available to higher consumers.

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Table 1. Calculations used for secondary production estimate for *Leuctra tenuis* in the hyporheic zone of Bull Creek. Equations are provided below column headings. Last four columns are offset because they represent measurements over the intervals between sampling dates.

Date	Density (No./m^2) N	Individual Dry Mass (mg) W	Biomass (mg/m^2) N×W	Individual Growth (mg) $\Delta W=W_2-W_1$	Mean Density (No./m^2) $(N_1+N_2)/2$	Interval P (mg/m^2) $\overline{N}\Delta W$	Daily P mg m^{-2}d^{-1} $\overline{N}\Delta W/\Delta t$
16 Feb	169.66	0.016	2.69				
				0.003	158.67	0.45	0.03
3 Mar	147.68	0.019	2.76				
				0.005	117.28	0.55	0.05
14 Mar	86.89	0.023	2.03				
				0.04	74.39	3.10	0.11
11 Apr	61.89	0.06	4.02				
				0.05	54.75	2.80	0.10
10 May	47.61	0.12	5.53				
				0.15	55.05	8.48	0.25
13 Jun	62.49	0.27	16.88				
				-0.03	49.99	-1.42	-0.05
13 Jul	37.49	0.24	9.07				
				0.07	24.10	1.71	0.06
10 Aug	10.71	0.31	3.35				
				0.08	6.25	0.51	0.01
15 Sep	1.79	0.40	0.71				

Table 2. Benthic secondary production estimates for *Leuctra* spp. above and hyporheic secondary production estimates for individual taxa below. Our data for *L. tenuis* is presented in both sections as a per area streambed (above) and a volumetric (below) estimate for comparison.

Species	Location	Habitat	Secondary Production	Source
Leuctra tenuis	Oklahoma, U.S.A	Benthic	0.033 g m^{-2} yr^{-1}	Jop & Stewart, 1987
Leuctra ferruginea	Prince Edward Island, Canada	Benthic	0.052 g m^{-2} yr^{-1}	Dobrin & Giberson, 2003
Leuctra spp.	Slovakia	Benthic	0.005 – 0.154 g m^{-2} yr^{-1}	Krno, 1997
Leuctra tenuis	Missouri, U.S.A.	Hyporheic (30-45 cm)	0.019 g m^{-2} yr^{-1}	Dorff and Finn, current study
Olinga feredayi (Trichoptera: Conoesucidae)	New Zealand	Hyporheic (30-45 cm)	6.462 g m^{-3} yr^{-1}	Wright-Stow et al., 2006
Acanthophlebia cruentata (Ephemeroptera: Leptophlebiidae)	New Zealand	Hyporheic (15-45 cm)	34.476 g m^{-3} yr^{-1}	Collier et al., 2004
Leuctra tenuis	Missouri, U.S.A.	Hyporheic (30-45cm)	0.126 g m^{-3} yr^{-1}	Dorff and Finn, current study

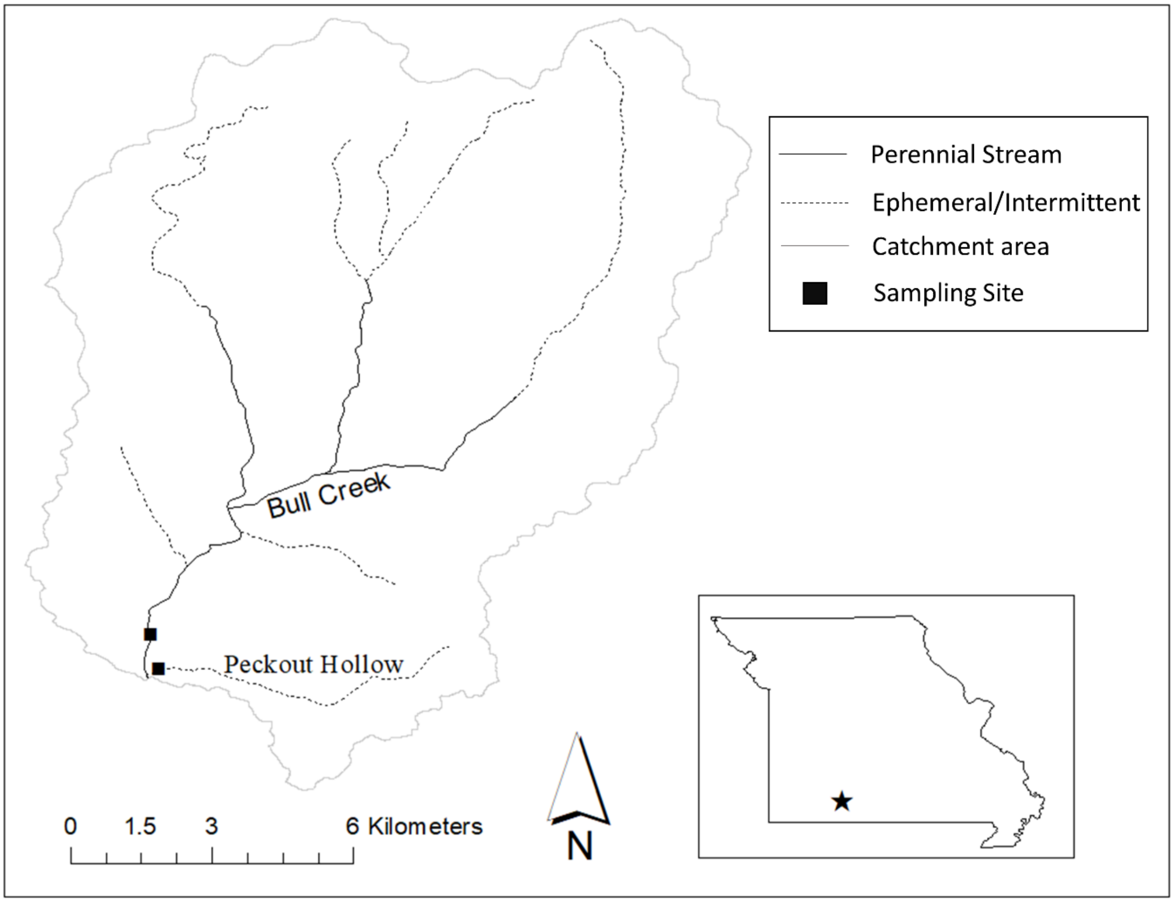

Figure 3. Map showing the location of field sites (black squares) and catchment area (grey line) of Bull Creek in southwest Missouri.

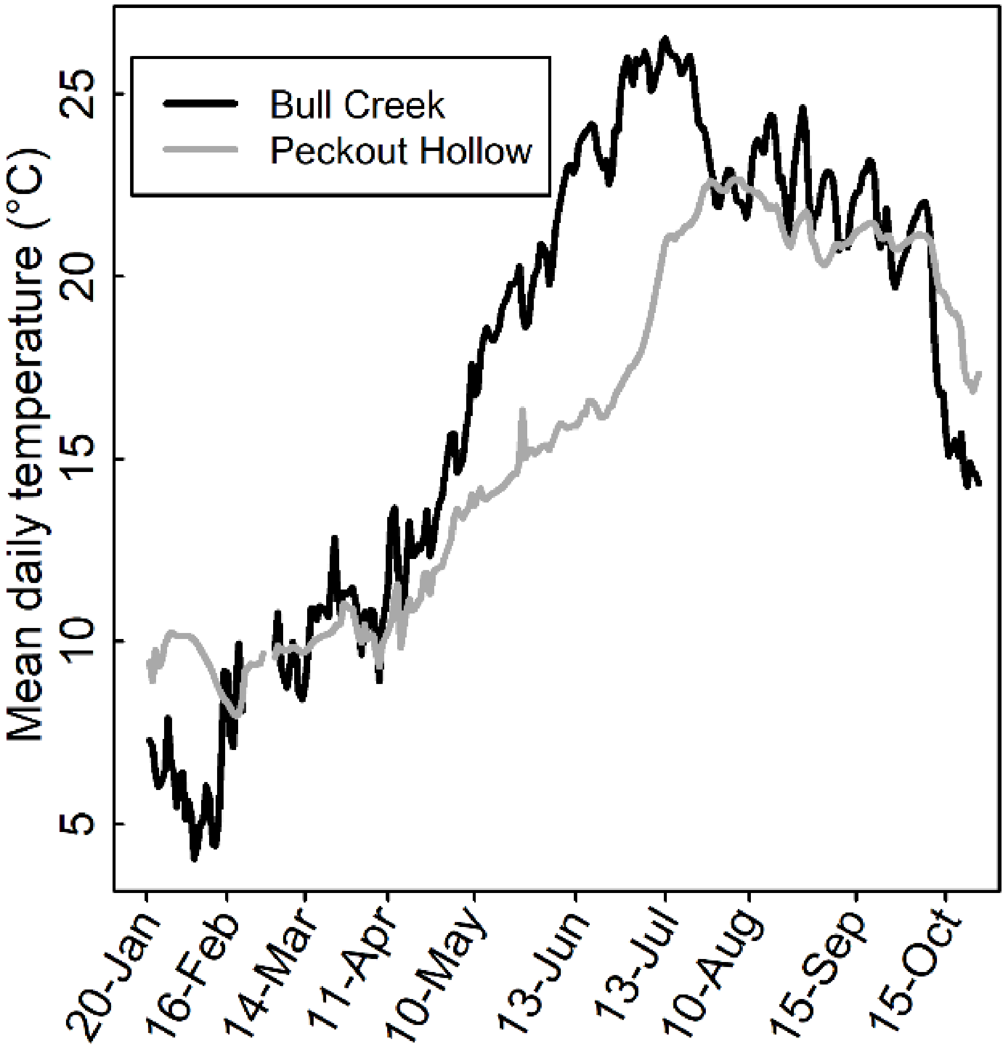

Figure 4. Mean daily temperature (˚C) through time in the hyporheic zones of Bull Creek and Peckout Hollow.

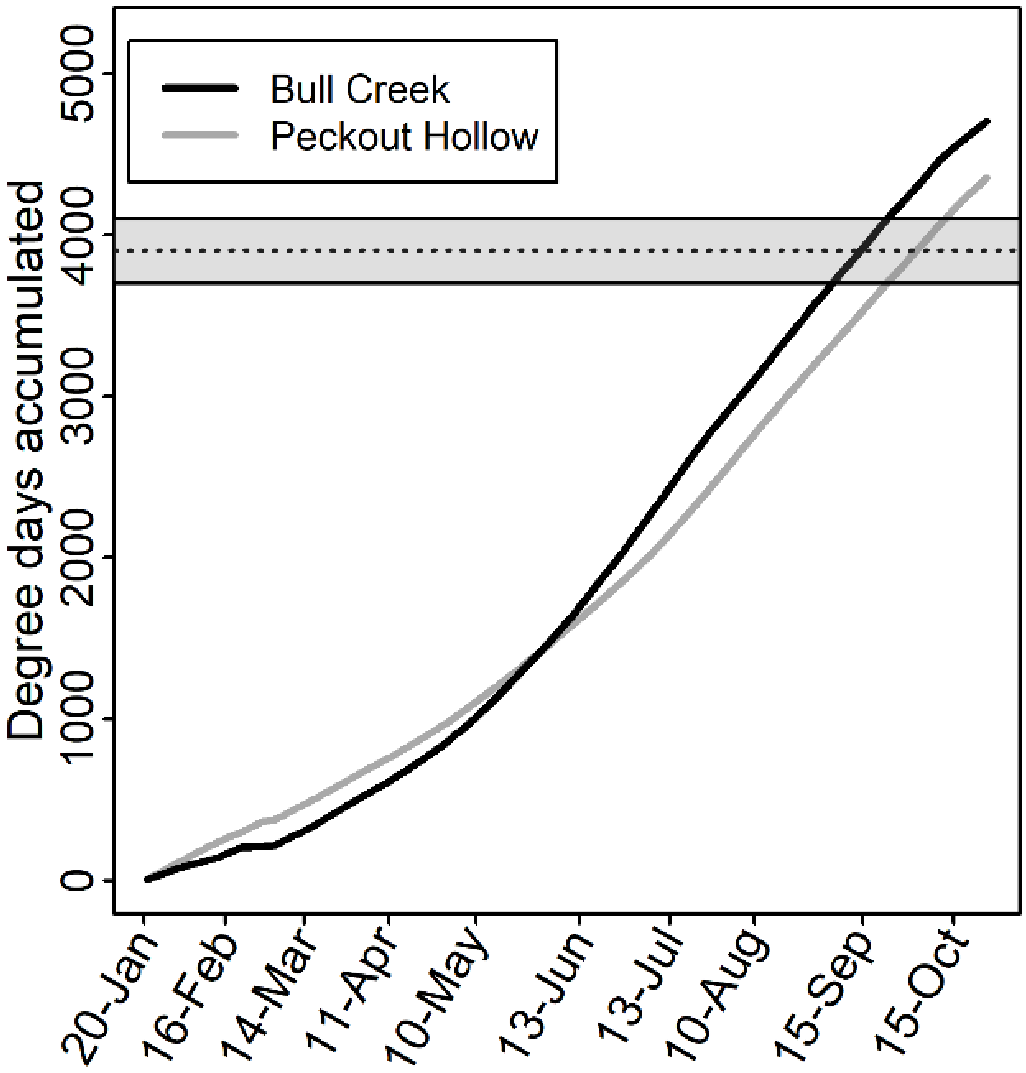

Figure 5. Accumulated degree days through time in the hyporheic zones of Bull Creek (black line) and Peckout Hollow (gray line). Dotted line and shaded area indicate approximate number of degree days until emergence of *Leuctra tenuis*.

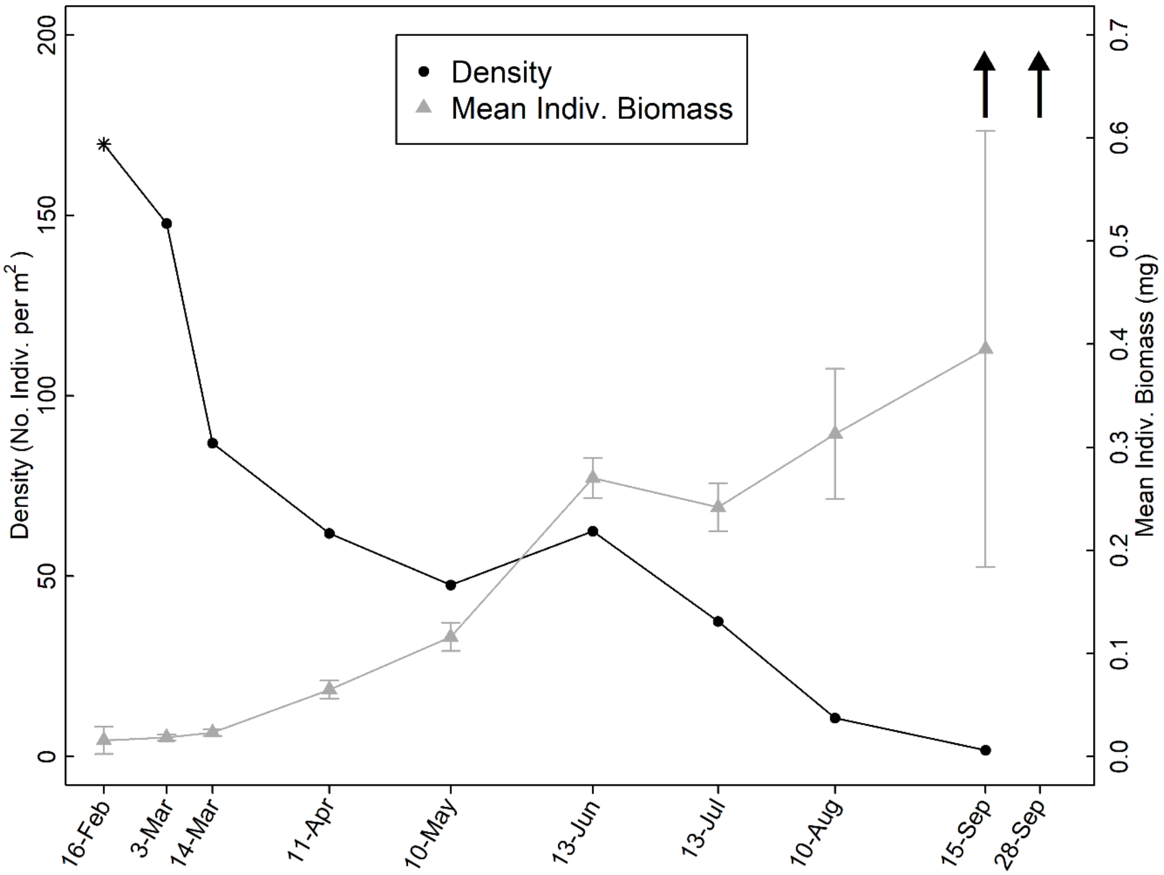

Figure 6. Density (number of individuals per square meter) and mean individual biomass (mg) of *Leuctra tenuis* in the hyporheic zone of Bull Creek through time (ordinal date). Black circles are density and gray triangles are mean individual biomass at each sampling date. Error bars for mean individual biomass are ±2 standard errors. Asterisk is an estimate of the density of the earliest instars. Black arrows indicate that adults were collected.

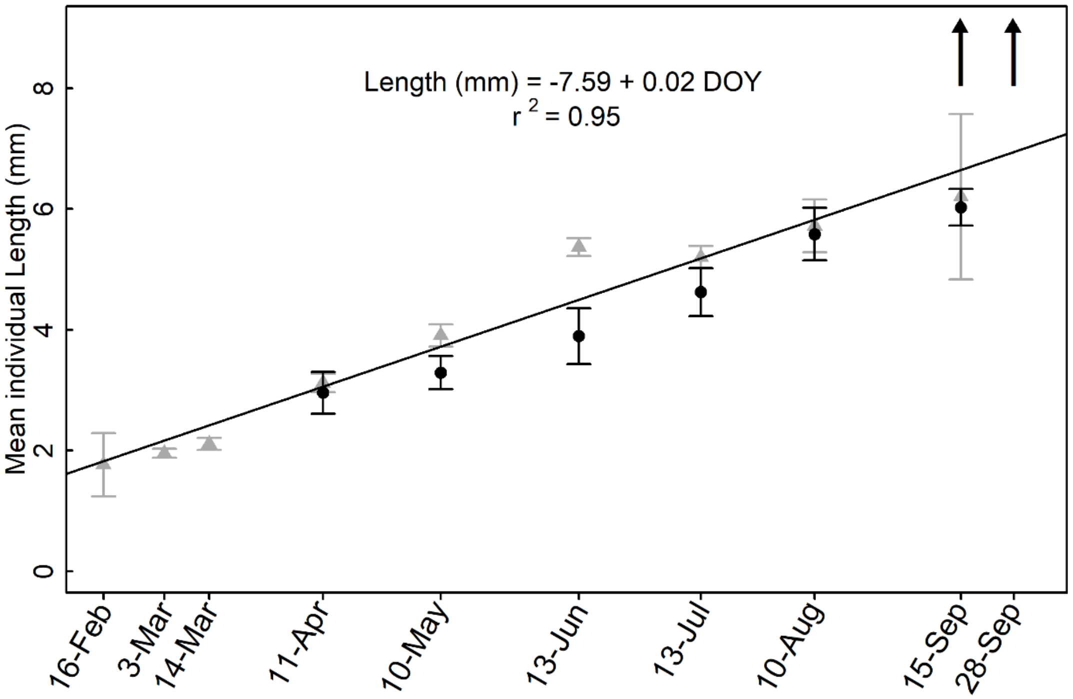

Figure 7. Mean length (mm) of *Leuctra tenuis* in the benthic and hyporheic zones through time (ordinal date). Gray triangles are average length of individuals from the hyporheic zone of Bull Creek. Black circles indicate average length of individuals collected and measured from benthic samples during the same dates. Error bars are ±2 standard errors. Earliest instars were never collected in the benthic samples. Black arrows indicate that adults were collected.

BENTHIC AND HYPORHEIC INSECT COMMUNITY COMPOSITION AND RESPONSE TO REPEATED FLOODS IN AN OZARK STREAM

Introduction

In ecology, discovering the processes that support species diversity and community composition remains a foundational question (Hutchinson, 1959; Tilman et al., 2014). Habitat heterogeneity and temporal variation are both essential abiotic aspects of ecosystems that drive community structure and diversity (MacArthur, 1958, 1975; MacArthur & Pianka, 1966). Another foundational goal of ecology is to uncover the processes that influence community stability through time (Gleason, 1926; Clements, 1936). Functional diversity appears to be one mechanism that supports community stability (Cummins, 1974; Laureto et al., 2015).

Streams are heterogeneous in three spatial dimensions and through time, making them dynamic systems (Ward, 1989). Temporal and spatial variability (e.g., habitat heterogeneity) are two of the main drivers of diversity within lotic systems (Horwitz, 1978; Stanford & Ward, 1983; Pringle et al., 1988; Ward, 1989; Poff & Ward, 1990; Bogan & Lytle, 2007). While foundational work has emphasized longitudinal (upstream-downstream) and lateral (channel-floodplain) connectivity in stream systems (Hynes, 1975; Vannote et al., 1980; Junk et al., 1989), less work has addressed the role of the vertical (surface-groundwater) spatial dimension of connectivity (Gibert et al., 1990; Boulton, 2007). A key component of vertical connectivity is the hyporheic zone, a unique habitat below the streambed surface. Hyporheic zones influence processes such as nutrient transformation and exchange, and they provide aquatic organisms with a unique ece (cf. Clements 1936, Stanford and Ward 1993, Boulton et al. 1998). The role of vertical connectivity in supporting distinct and diverse communities through time has been investigated, but the results of such studies are often inconsistent across stream systems (see Dole-Olivier 2011 for review).

Aquatic macroinvertebrates are ubiquitous, diverse, and a key component of stream ecosystems (Merritt et al., 2008). Some macroinvertebrates are obligate hyporheic inhabitants, requiring the hyporheic zone to complete their development (Stanford & Gaufin, 1974; Stanford & Ward, 1988), while others use the hyporheic zone temporarily as a refuge from extreme flow conditions (e.g., flood and drought, Dole-Olivier et al. 1997, Wood et al. 2010, Vadher et al. 2017). The existence of the hyporheos, the fauna that occupy the hyporheic zone, has been confirmed throughout the world (Coleman & Hynes 1970; Bishop 1973; Danielpol 1976; Hynes et al. 1976; Stanley & Boulton 1993; Xu et al. 2012) and across the United States (Stanford & Gaufin, 1974; Poole & Stewart, 1976; Pennak & Ward, 1986; Strommer & Smock, 1989; McElravy & Resh, 1991; Stanley & Boulton, 1993). However, few studies of the hyporheos have been conducted in the Ozark Highlands ecoregion (Hunt, 1999; Hunt & Stanley, 2003; Distefano et al., 2009), a region containing streams with coarse gravel beds with large interstitial spaces that form deep hyporheic zones. Many Ozark streams are also classified as flashy with floods quickly following rainfall events (Leasure et al., 2016). The rapid rise in stream flow may elicit a behavioral response in aquatic macroinvertebrates causing them to migrate into the hyporheic zone to avoid being washed downstream (Stubbington, 2012).

Although macroinvertebrates are taxonomically diverse, there can still be considerable overlap of functional traits among taxa (Cummins, 1974; Poff et al., 2006). Functional classification of organisms is based on biological or ecological traits (e.g., life-history strategies, trophic position, morphology) that are a result of natural selection over ecological timescales (Poff et al., 2006). Functional overlap creates redundancies (i.e., two taxa that occupy similar trait space, Rosenfeld 2002) that support more resilient communities by allowing functionally similar taxa to replace others in the face of perturbation (Hemphill & Cooper, 1983; Bogan & Lytle, 2007; Boersma et al., 2014; Vander Vorste et al., 2015). Functional redundancies, which might result in direct competition, are often separated by space (habitat heterogeneity) and time (seasonal variation). In other words, temporal separation (e.g., phenology) or spatial separation (e.g., habitat preference) can separate two functionally similar taxa. In frequently disturbed systems such as streams, functional redundancy likely helps maintain diverse communities and functioning ecosystems by creating resilience within the community (Poff et al., 2006).

I studied two reach types (gravel-bed vs. bedrock-lined) in an Ozark stream that experienced the same flow regime and had the same regional species pool but differed in extent of vertical connectivity. I monitored benthic insect community composition and response to flood disturbance and concurrently monitored the hyporheic insect community in the gravel-bed reach. I used the data collected to test three major hypotheses: **(H1)** vertical connectivity supports larger densities and diversity of insects through time, **(H2)** bedrock-lined and gravel-bed reaches support distinct communities of insects but gravel-bed communities will be more stable through time due to vertical connectivity to refugium, and **(H3)** the presence of a hyporheic insect community supports greater resilience to flooding within the entire gravel-bed reach community. I also asked whether functional diversity was significantly different among gravel, bedrock, and hyporheic communities.

Methods

I monitored benthic and hyporheic insect communities in Bull Creek (Fig. 8), a headwater stream located in southwest Missouri in the Ozark Highlands ecoregion (hereafter

Ozarks). Bull Creek is designated as an outstanding state resource water (MO DNR, 10 CSR 20-7) and at the study reach is located in a minimally impacted watershed composed largely of Mark Twain National Forest. Bull Creek originates on the south side of the Springfield plateau at approximately 420 m elevation and flows southwest through Christian and Taney Counties before flowing into Lake Taneycomo at approximately 213 m elevation. The watershed draining into the study reach is approximately 100 km^2. Annual mean discharge of Bull Creek at the study reach is 1.32 m^{3}s^{-1} (from data collected at a USGS gauge approximately 25 km downstream and corrected using a factor provided by Claudio Meier, personal communication). Floods are relatively common in Bull Creek, which is classified as a groundwater-flashy system (Leasure et al., 2016). USGS data collected over a period of 25 years shows 13 floods that exceeded 10,000 cfs (ca.285 m^{3}s^{-1}). Floods can occur at any time of year, but larger magnitude floods are more common between March and June (Claudio Meier, personal communication). Two floods that were greater than 285 m^{3}s^{-1} occurred during the sampling period (Table 3). Flood events that meet or exceed ca. 285 m^{3}s^{-1} scour the streambed in bedrock-lined sections, mobilize the substrate in the gravel-bed sections of the study reach, and substantially exceed bank full (personal observation).

Bull Creek at the study reach alternates between bedrock-lined reaches with limited (<10 cm) or no hyporheic zone and gravel-bed reaches with extensive hyporheic zone (up to and potentially greater than 2 m depth). Within the gravel-bed reaches lateral and medial gravel bars form in the stream channel. Hyporheic flow is associated with these gravel bars and contributes to greater availability of hyporheic habitat (Poole et al., 2002, 2006).

From October 2017 to September 2018, I collected benthic Surber samples (30 cm x 30 cm frame, 500 µm mesh) monthly from a gravel-bed and a bedrock-lined reach (hereafter gravel and bedrock, respectively) that were separated by approximately 350 meters in the stream. I collected a total of seven Surber samples during each sample date: three from a riffle at the gravel reach and two each from one small upstream riffle and one small downstream riffle at the bedrock reach. I also added an opportunistic sampling event in the gravel reach and the hyporheic habitat 9 days after the peak magnitude of a late February flood. Because I did not also sample the bedrock reach during the opportunistic sampling event, I did not include the samples for the quantitative analysis over the entire year of data. Instead, I used them for post-flood comparisons between gravel and hyporheic habitats as well as for qualitative data. Samples were stored in 95% ethanol and brought back to the lab for processing.

During the same sampling dates, I also collected replicate hyporheic samples at the gravel reach. I sampled the hyporheic zone using a modified Bou-Rouch pump, which has been used successfully to sample the hyporheos (Bou & Rouch, 1967; Hunt & Stanley, 2000; Boulton et al., 2003). I used a pitcher pump modified with plumbing fittings that could be moved from one well to another allowing for rapid and easy replicate samples to be collected. Polyvinyl chloride (PVC) wells with 15 cm of 5 mm perforations (the screen) at one end were driven to a depth 45 cm so that the screen was at a depth of 30-45 cm. I installed three wells (7 m stream distance apart) in each of three locations of the gravel reach: medial gravel bar, in a riffle below the gravel bar (downstream), and in a riffle above the gravel bar (upstream). I pumped 8 L of hyporheic water from each well at approximately 16 L/min as pumping rate has been shown to affect invertebrates collected (Hunt & Stanley, 2000) and filtered out invertebrates using a 180 µm sieve. Samples were stored in 95% ethanol and brought back to the lab for processing.

In the lab, benthic and hyporheic insects were sorted and identified to finest taxonomic level practical (usually genus) using available taxonomic keys and a dissecting scope. Although other aquatic invertebrates were collected in all sample types, I looked at only insect taxa. Invertebrate taxa that were excluded in my analyses included crustaceans (typically Isopoda and Copepoda, but also Decapoda) and snails (Gastropoda). Non-insect invertebrates were removed from analyses because I was specifically interested in monitoring the response of aquatic insects and because densities of these organisms were relatively low (with the exception of snails). Additionally, time constraints precluded identification beyond very coarse taxonomic groups. Five bedrock Surber samples with insect abundances exceeding 1000 individuals were subsampled (1/2–1/8) using a Wildco® Folsom Plankton Splitter until a minimum of 500 individuals were processed. Unprocessed portions of split samples were sorted to remove large and/or rare taxa.

For temporal comparisons of density and diversity, I combined monthly data from Surber samples from each habitat into a single replicate, and for within month spatial comparisons I treated each Surber sample as a replicate. To facilitate community comparisons between seasons, I defined a pre-flood period ('dry season') from October to February and a post-flood period ('wet season') from March to September.

To assess whether differences in mean annual density and mean annual taxonomic richness between gravel and bedrock reaches were statistically different, I used Welch two sample *t*-tests ($\alpha = 0.05$) in R v3.3.3 (R Core Team, 2017). I calculated Shannon diversity for each of the three habitats and ran rarefaction using the vegan package in R (Oksanen et al., 2018), and used *t*-tests to compare whether annual means were statistically different. Because sampling effort was different between bedrock and gravel reaches (3 vs. 4 Surber samples) and sampling technique was different between benthic and hyporheic (Surber vs. pump), I ran rarefaction on the community data from each of the habitat types by randomly resampling individuals from the community matrix. Rarefaction allows comparison of species richness among disparate sampling techniques in order to assess whether observed differences are real or are due to differences in sampling effort (Gotelli & Colwell, 2001).

To look at temporal patterns of community structure, I ran non-metric multidimensional scaling (NMS; Kruskal 1964, Mather 1976) with Sørenson distance as the measure of dissimilarity on the community data using PC-ORD software (McCune & Mefford, 2011). Community data were monthly means of the 3 to 4 replicate Surber samples that were log-transformed after testing for normality. I also compared correlation coefficients with axes 1 and 2 for individual taxa in the NMS 2-dimensional solution to determine which taxa were influential in separating samples in ordination space. To test for differences in benthic communities between habitats across the entire year as well between seasons (wet and dry), I ran multi-response permutation procedures (MRPP) in PC-ORD using Sørenson distance. MRPP is a non-parametric procedure to test for significant differences between groups (Mielke & Berry, 2001) and provides a measure of effect size (*A*) and a *P*-value.

To understand patterns of functional diversity, I looked at functional feeding group (FFG) and four other traits of insects that I hypothesized *a priori* to be relevant to resistance or resilience to flow disturbance in the benthic habitat types or that might facilitate use of hyporheic habitat. The traits I selected were primary habit, body shape, body size, and armor (degree of sclerotization). Trait information came from the USGS database (Vieira et al., 2006) and Merritt, Cummins, & Berg (2008). The non-biting midges (family Chironomidae) were not included in the FFG analyses because finer taxonomic resolution required for trait classification in this family is difficult and time-consuming (Merritt et al., 2008). I calculated relative abundance of combined Surber samples across the year for each of the five trait types and compared them among all habitat types (gravel, bedrock, and hyporheic). I tested for annual differences between individual trait types among habitats using analysis of variance (ANOVA) and Tukey's tests. Because I ran multiple comparisons (66) of functional traits among habitat types, I used the Bonferroni correction to set a lower critical value ($\alpha = 0.05/66 = 0.0008$).

For summary analysis of functional diversity, I used the FD package in R (Laliberté & Legendre, 2010; Laliberté et al., 2014). The FD package uses a species by trait matrix for each sample site and date to calculate Euclidean distances, analyzes the distances using Principal Coordinates Analysis (PCoA; Gower 1966), and then uses the PCoA axes as new traits to compute functional diversity indices. Using PCoA allows for comparisons between communities by combining all of the functional traits from the analysis into a single parameter for each sample. I calculated functional richness, functional evenness, and functional dispersion using FFG, primary habit, body shape, body size, and armor within all three habitat types and all sample dates. Functional richness represents the volume of functional space that a community takes up in functional space and is calculated using presence-absence data and all five traits listed above. Functional evenness uses relative abundances of community data and represents the evenness of the distribution of functional traits. Functional dispersion represents how spread out the community is in the functional trait space and is the mean distance of all individual species from the centroid in the functional trait space. The functional diversity analyses were used to answer whether a more functionally diverse community in the gravel reach supports community resilience to flooding.

Results

Densities of insects were highly variable through time in the bedrock reach, spiking to as high as 49,522 individuals per square meter in one Surber sample in August and as low as 122 individuals per square meter in an April sample, 11 days after a flood event (Fig. 9). Annual mean density in the bedrock reach was 5,584 individuals per square meter (CV = 1.67). Densities in the gravel reach were smaller but less variable through the months (CV = 0.85) with an annual mean of 2,590 individuals per square meter. Because of the high degree of variability in the bedrock reach, annual mean densities were not significantly different ($t = 1.92$, df = 13.4, $P = 0.08$).

Monthly mean taxonomic richness of insects was generally greater in the gravel than in the bedrock reach (Fig. 10). Annual mean taxonomic richness was significantly different ($t = -3.29$, df = 21.37, $P = 0.003$) in the gravel than in the bedrock reach (16.22 and 11.31, respectively). Mean annual hyporheic insect richness was 3.29, and monthly sample means were almost always less than the other two habitat types (gravel and bedrock). However, hyporheic taxa richness was not significantly different ($t = 0.35$, df = 3.45, $P = 0.74$) from bedrock taxa richness when sampled post-flood in March, and hyporheic taxa richness was significantly greater ($t = 3.69$, df = 9.10, $P = 0.005$) than bedrock taxa richness when sampled after the second flood in April.

The opportunistic sampling event (3 March 2018, not shown in figures) in the gravel habitat showed a change (although not significant) in mean taxa richness (from 11.25 on 16 February to 8 on 3 March) in the benthic zone, while insect taxa richness in the hyporheic zone changed significantly ($t = -2.42$, df = 11.01, $P = 0.03$) from 2.67 on 16 February to 6.67 on 3 March. Several taxa (e.g., *Maccaffertium* and *Stenacron*, both heptageniid mayflies, and

Neoperla, a perlid stonefly) that were previously undetected in the hyporheic zone were present in the post-flood hyporheic samples. Aside from the post-flood changes in hyporheic taxa richness, I also repeatedly detected two insect taxa in the hyporheic zone that were never found in benthic samples (*Corethrella* and *Sialis*). Other taxa (e.g., *Argia, Gomphus,* and *Leuctra*) were found consistently, but not exclusively, in the hyporheic zone.

Rarefaction results (Fig. 11) suggest that as long as approximately 500 individuals are collected, the differences in species richness between hyporheic and benthic habitats are real and not a result of collection method. As long as 1000 individuals are sampled from gravel and bedrock, the difference in species richness between these benthic habitats are real and not a result of sampling effort. With the exception of December to February pre-flood samples, counts exceeded 500 individuals in the hyporheic samples each month over the sampling period.

Shannon diversity throughout the year was greater in the gravel reach than in the bedrock reach with the exceptions of October and February sampling events, in which Shannon diversity was indistinguishable between these habitats, and in August when Shannon diversity was smaller in the gravel reach (Fig. 12). The August sampling event corresponded to the driest sampling date and the lowest surface flow. Annual mean Shannon diversity was 2.11 in the gravel reach, which was significantly different (t = 3.12, df = 20.61, $P = 0.005$) than mean annual Shannon diversity in the bedrock reach, 1.59. In the hyporheic zone, insect Shannon diversity was consistently smaller (annual mean = 0.73) than in benthic habitats, similar to the pattern observed for insect taxa richness.

Non-metric multidimensional scaling generated a stable 2-dimensional solution with log-transformed community data from bedrock and gravel reaches (stress = 0.13, instability = 0.00001; Fig 13). The two axes represented 83% of the variation between samples (axis 1: r^2 =

0.397, axis 2: $r^2 = 0.434$). MRPP on the dry season communities (October to February, roughly outlined by ellipses in Fig 13) showed a significant difference between gravel and bedrock habitats ($A = 0.23$, $P = 0.0016$). Communities between bedrock and gravel habitats were also significantly different during the wet season ($A = 0.04$, $P = 0.04$). The insect communities in the gravel and bedrock reaches both changed following the initial flood event in February, but the bedrock community may have been more impacted by the first flood. The community in the bedrock reach appeared to be so greatly impacted from the first flood that changes to the community were minimal following the second flood. More drastic post-flood changes in the bedrock reach were supported by the proximity of March and April bedrock communities in ordination space as well as by taxonomic richness and densities of insects, which both decreased substantially after the first flood. For instance, mean insect densities in the bedrock reach plunged from 11,788 in February to 1,994 individuals per square meter in March after the first flood. Conversely, shifts in the community still occurred in the gravel reach after both floods, indicating that the community was still changing in composition. Recovery to pre-flood community structure along NMS axis 2 in the gravel reach happened quickly (<1 month after flood) versus the bedrock reach, in which community structure continued to fluctuate >3 months post-flood. Considerable mixing of the insect community occurred following both floods. For instance, the gravel community in April closely resembled the dry season bedrock community, and the bedrock community in May resembled the dry season gravel community. Indeed, MRPP revealed that across the entire year bedrock and gravel communities were not significantly different ($A = 0.003$, $P = 0.32$), as evidenced by the ordination plot in which points from both benthic communities are scattered across the non-dimensional space. Nevertheless, when looked at seasonally (dry vs. wet) the benthic communities were significantly different.

Correlations of individual taxa to the axes of the ordination revealed differences in dry season community compositions between gravel and bedrock habitat types (Table 4). Insect taxa with strong positive correlations to axis 1 (e.g., *Maccaffertium* and *Neoperla*) showed that these taxa potentially have habitat preferences met by the gravel reach. However, strong negative correlations with axis 1 (e.g., *Hydropsyche* and *Simulium*) showed the potential preference of these taxa to the bedrock reach. A strong positive correlation with axis 2 (e.g., *Caenis*) may show a seasonal variation of taxa through time, possibly associated with phenology.

There were significant differences in proportions of the different FFGs among habitats (Fig. 14). Proportion of collector-gatherers in the hyporheic habitat was significantly different ($P < 0.00004$) from both gravel and bedrock habitats. Proportion of predators in the gravel habitat was significantly different ($P < 0.0003$) from the bedrock and hyporheic habitats. Proportion of scrapers was significantly different ($P < 0.0001$) between gravel and hyporheic habitats with most scrapers preferring the former. Proportion of the community composed of midges in the hyporheic habitat was significantly different ($P < 0.0003$) from gravel and bedrock habitats. There were no significant differences in proportion of collector-filterers and shredders among habitats.

The body shape trait revealed some additional patterns (Fig. 15A). Proportion of dorsoventrally flattened insects in the gravel habitat was significantly different ($P < 0.00001$) from the hyporheic and bedrock habitats. The proportion of tubular-shaped insects in the gravel reach was significantly different ($P < 0.00001$) from both bedrock and hyporheic habitats. There were no significant differences in the proportions of bluff-blocky and streamlined-fusiform insects among habitats.

There were significant differences in body sizes among habitats as well (Fig. 15B). The proportion of insects classified as small was significantly different ($P < 0.00001$) between the gravel and hyporheic habitats, while the proportion of medium-sized insects in the gravel habitat was significantly different from the hyporheic habitat ($P < 0.00001$). Significantly more ($P < 0.0002$) of the insect community was made up of large-sized individuals in the gravel habitat than in bedrock habitat.

For the primary habit traits, burrowers showed significant differences ($P < 0.0005$) among all three habitat types (Fig. 15C). The proportion of burrowers was greatest in the hyporheic habitat and smallest in gravel habitat. The proportion of clingers in the gravel habitat was significantly different ($P < 0.0005$) from the bedrock or hyporheic habitats. The proportion of sprawlers was significantly different ($P < 0.00002$) between the hyporheic and bedrock habitats. Climbers, skaters, and swimmers showed no significant differences among habitat types and was most likely due to underrepresentation of the trait types.

For armor, proportion of insects that were fully-armored and proportion that were partly-sclerotized were significantly different ($P < 0.00001$) between the gravel and hyporheic habitats (Fig. 15D). Significant differences ($P < 0.00001$) in proportion of unarmored individuals were also present between the hyporheic and bedrock insect communities.

Functional richness was generally greater across the sampling period in the gravel habitat than in the other habitats (Fig 16A). The functional richness of the bedrock community decreased abruptly following flood events, which mirrored decreases in taxonomic richness. Functional evenness was highest in the hyporheic habitat and lowest in the bedrock habitat at the beginning of the study period (Fig 16B). However, functional evenness seemed to converge at moderate values across all three habitats following floods. Functional dispersion was lowest in the hyporheic habitat and highest in the gravel habitat throughout the study period (Fig 16C).

Discussion

Densities of insects across the entire year were not significantly different between bedrock and gravel reaches and therefore the first part of **H1** (i.e., that more vertical connectivity will lead to larger densities of insects) is rejected. Within the bedrock reach densities fluctuated between extremely large to near zero following repeated flood events. Part of the fluctuations in densities in the bedrock reach were likely due to patchiness of distribution. There were areas of moss (Bryophyta) along the stream margins that contained higher concentrations of several common taxa, notably Chironomidae and Hydropsychidae (personal observation). High densities of aquatic insects in moss-covered rock habitat have been reported elsewhere (Gurtz & Wallace, 1984), and moss patches may act as fine-scale flow refugia (Huttunen et al., 2017; Wulf & Pearson, 2017). The lack of refugia other than moss patches and several cracks and crevices in the bedrock itself likely resulted in the extreme response of insect densities, especially following the first flood. Densities of insects in the gravel reach were more stable through time than in the bedrock reach. Although densities in both benthic habitats decreased post-flood, they rebounded more rapidly in the gravel than in the bedrock reach.

In support of the second part of **H1** that insect diversity is greater when there is greater extent of vertical connectivity, insect richness and Shannon diversity were almost always greater in the gravel than in the bedrock reach. Additionally, both benthic habitats had consistently greater insect richness than the hyporheic habitat. The results of the rarefaction indicated that these differences were real and not simply a result of variation in sampling effort or technique. I believe that the greater taxonomic richness in the gravel reach was due to the presence of a diversity of substrate sizes (e.g., gravel and cobble) that create more habitat heterogeneity and vertical connectivity. Conversely, the reduced richness in the bedrock reach is potentially due to homogeneity of habitat with only two main microhabitats available, moss or bedrock. Although substrate stability is a well-recognized driver of insect diversity and density (Minshall, 1984; Poff & Ward, 1990), there seems to be an optimal or intermediate degree of stability to support more diverse communities (Connell, 1978; Minshall, 1984; Townsend & Scarsbrook, 1997; Cobb et al., 2008).

Stream macroinvertebrate community composition and response to disturbance can be driven by differences in substrate (Gurtz & Wallace, 1984; Minshall, 1984; Quinn & Hickey, 1990; Holomuzki & Biggs, 2000). In partial support of **H2**, this study found that there were unique communities between gravel and bedrock reaches in the same stream during both dry and wet seasons, but that repeated floods mixed community composition across habitat types. The hyporheic insect community over the same sampling period, although not as diverse as the two focal benthic habitats, was relatively stable through time and flow disturbance.

The hyporheic insect richness was relatively depauperate compared to the benthic habitat type. Ozark streams are flashy (Leasure et al., 2016) and flood events can cause massive bed-movement events (Palmer, 1993). Although the interstitial spaces created by these gravel-beds may be extensive, the stability of the streambed may limit the diversity and abundance of the hyporheos. In other words, the hyporheic habitat may be too evanescent to allow for development of a more diverse and abundant insect community. Meiofauna groups (consisting mainly of Copepoda and Isopoda) were far more abundant in the hyporheic zone, which is not uncommon and has been reported elsewhere (Strommer and Smock 1989, Boulton et al. 1998, 2003). Because of taxonomic difficulty and limitations on time, the meiofauna were not included in the current study. However, meiofauna have the potential to be diverse and abundant in the hyporheic zone, and may contribute substantially to whole-stream secondary production (Huryn 1996, Stead et al. 2004, Wright-Stow et al. 2006, Dorff and Finn unpublished data).

The two insect taxa (*Corethrella* and *Sialis*) detected repeatedly and exclusively in the hyporheic zone are both predators. *Corethrella* (Diptera: Corethrellidae) are frog-biting midge larvae that have been found in the hyporheic zone in at least one other ecoregion (Boulton et al., 1992), but the larvae in the hyporheic samples from this study do not match any of the current descriptions for North American species (McKeever and French 1991, Art Borkent, personal communication). It is likely that this is an undescribed species of *Corethrella* that appears to require the hyporheic zone for its development. Larval *Sialis* (Megaloptera: Sialidae) or alderflies are relatively large (10-20 mm) insects that inhabit sediments (Merritt et al. 2008, Chapter 16). While not surprising, this represents the first known collection of these larvae in the hyporheic zone. Although *Corethrella* and *Sialis* were only collected in hyporheic zone and not benthic samples during the entire sampling period, I did not sample all habitat types within this stream (e.g., pools or slack waters), and so it is possible that these taxa are present elsewhere in the stream system and not exclusively hyporheic. Other taxa (e.g., *Argia* and *Leuctra*) were found consistently, but not exclusively, in the hyporheic zone. The presence of unique (potentially obligate) hyporheic insect taxa and facultative hyporheic taxa lends weight to the argument that vertical connectivity supports greater insect diversity in Ozark streams (**H1**).

The presence of previously undetected taxa in the hyporheic samples post-flood is potentially an indication of the use of the hyporheic zone in Bull Creek as a flow refugium. However, insects may have simply been redistributed as a result of associated bed movement during the floods. In other words, colonization of the hyporheic zone might occur actively and/or passively. Marmonier & Creuzé des Châtelliers (1991) documented increases of lentic and lotic organisms in the hyporheos following a flood and suggested that the interstices act as a "trap" for the lentic organisms and as a potential source of recolonization for the lotic benthos. Whether the taxa in the present study were washed into the hyporheic zone during the flood or whether they actively migrated downwards in response to the flood remains to be investigated.

Studies also have monitored concurrently benthic and hyporheic community response following disturbance. For instance, Stubbington et al. (2014) found that benthic taxa richness decreased during extreme drought, but hyporheic taxa richness remained relatively unchanged. The authors suspected that the relatively stable abiotic conditions within the hyporheic zone accounted for these differences. In an intermittent river in France, Datry (2012) found that both benthic and hyporheic densities and taxonomic richness decreased following drying, but that decreases were more pronounced for the benthic community. Descloux et al. (2013) found that fine sediment deposition into streams in France affected both the benthic and hyporheic invertebrate communities, decreasing densities and taxa richness. Vander Vorste et al. (2016) found that benthic macroinvertebrate communities were highly resilient to stream drying with taxonomic richness and densities recovering within 1 to 2 weeks, which supported the idea of recolonization from the hyporheic zone.

Heterogeneous physical substrate tends to lead to more functionally diverse benthic invertebrate communities and contributes to the resilience of the community in the face of disturbance (Gurtz & Wallace, 1984; Statzner & Resh, 1993; Allan, 2004; Frady et al., 2007). Invertebrates that use the hyporheic zone have been classified functionally (Claret et al., 1999; Robertson & Wood, 2010) and studies have monitored functional response to disturbance in the hyporheic zone. For instance, Vadher et al. (2017) observed the response of five species of benthic macroinvertebrates in experimentally dried mesocosms and showed that most invertebrates with traits relevant to subsurface movement were able to exploit the hyporheic refuge and avoid desiccation. Stubbington (2012) looked at several macroinvertebrate traits (e.g., burrowing) that might facilitate macroinvertebrate use of the hyporheic zone as a refuge and identified midges (Chironomidae) as possessing many of these traits. In the present study, midges dominated in the hyporheic habitat, which drove many of the patterns observed in functional diversity. For instance, midges accounted for larger proportions of tubular body form, smaller body size, and primarily burrower habits. Midges can be a dominant component of the hyporheic insect community, and their contribution to secondary production in the hyporheic zone has been shown to be substantial with >37% of total midge production occurring below 10 cm depth (Reynolds & Benke, 2012).

Functional richness, functional evenness, and functional dispersion declined most evidently in the bedrock community post-flood. Although evenness and dispersion in the bedrock habitat peaked following the first flood, this was probably due to reduction in the abundances of dominant taxa. Both metrics decreased following the second flood. The functional richness of the hyporheic insect community increased following the first flood, which again could be an indication of the passive or active occupation of this habitat post-flood. In support of **H3**, the gravel community had consistently greater functional richness and dispersion than the bedrock community, which is an indication of a more functionally diverse and stable community, possibly driven by habitat heterogeneity and vertical connectivity. Although the hyporheic community seemed to be more functionally resilient than the bedrock community, this could have been a result of the abiotic stability of the habitat (e.g., temperature; Stubbington et al., 2014). I treated functional composition simply as a proportion of the total insect community. However, a potentially better way to look at this may be the proportion of biomass that these groups account for within the total community (Benke & Huryn, 2010). For instance, midges comprise a large proportion of the insect community, but their relatively small individual biomass may moderate their influence on the functional composition of a community in terms of biomass.

Ozark streams that possess extensive gravel beds have high potential for hyporheic contribution to instream processes and they likely contribute to community resilience. Ozark streams are subject to extreme flooding as well as drying events with entire reaches capable of losing surface flow during dry summer months. Nevertheless, dynamic stream systems are still capable of maintaining relatively high diversity and biomass (Lancaster & Hildrew, 1993). The Ozarks remains an understudied region with respect to aquatic ecology, and especially hyporheic ecology. Only a few studies have looked at the composition or the response to disturbance of the hyporheos in the Ozarks (Hunt, 1999; Distefano et al., 2009). With the potential of the hyporheic zone to serve as a refuge, a source of community resilience, and its support of a unique community, further study of hyporheic ecology in the Ozarks could help answer foundational ecological questions.

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Table 3. Dates of floods over the past 4 years in Bull Creek exceeding 285 m^3s^{-1} at gauging station downstream of study site. Magnitude of individual flood events in m^3s^{-1}. Corresponding dates (where applicable) of pre- and post-flood sampling events.

Flood Date	Previous Flood	Pre-flood Sample	Post-flood Sample	Peak Discharge
22 April 2017	482 days	NA	NA	308.7 m^3 s^{-1}
30 April 2017	8 days	NA	NA	926 m^3 s^{-1}
24 February 2018	300 days	16 February 2018 8 days	14 March 2018 18 days	427.6 m^3 s^{-1}
27 March 2018	31 days	14 March 2018 13 days	11 April 2018 15 days	297.3 m^3 s^{-1}

Table 4. Pearson's correlations (r) between genera of insects and the corresponding axis on the NMS plot.

NMS axis	Taxon	r-value
Axis 1	*Microcylloepus*	0.50
	Psephenus	-0.58
	Chironomidae	0.59
	Hemerodromia	0.53
	Antocha	0.68
	Simulium	0.65
	Acentrella	0.60
	Maccaffertium	-0.77
	Gomphus	-0.67
	Neoperla	0.70
	Acroneuria	0.70
	Ceratopsyche	0.55
	Hydropsyche	0.74
Axis 2	*Microcylloepus*	-0.50
	Optioservus	-0.66
	Stenelmis	-0.66
	Psephenus	-0.56
	Atherix	-0.58
	Bezzia/Palpomyia	-0.51
	Chironomidae	-0.56
	Hemerodromia	-0.58
	Caenis	-0.75
	Tricorythodes	-0.62
	Helicopsyche	-0.65
	Ochrotrichia	-0.57
	Oecetis	-0.53

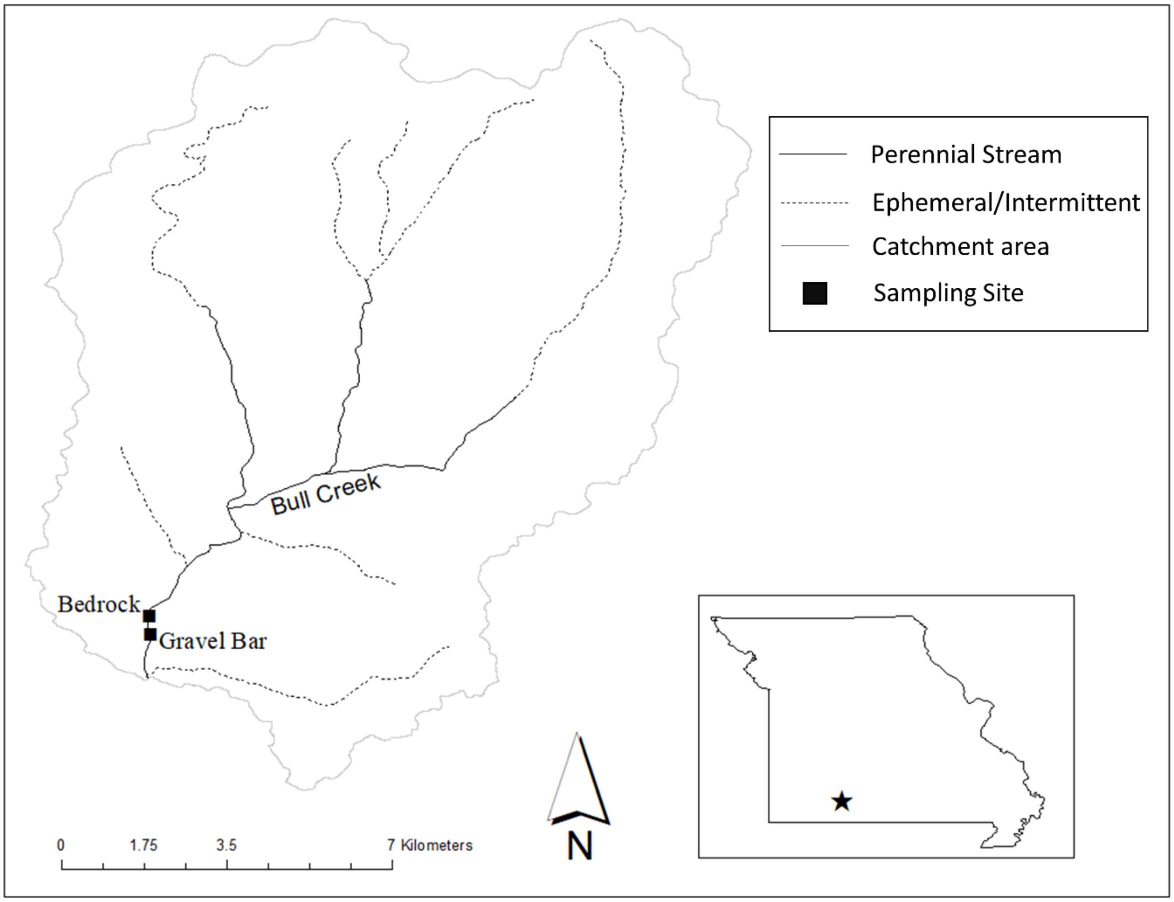

Figure 8. Map showing the location of Bull Creek, as well as the drainage area and stream network at the study site. Approximate locations of bedrock and gravel-bed reaches are marked with black squares.

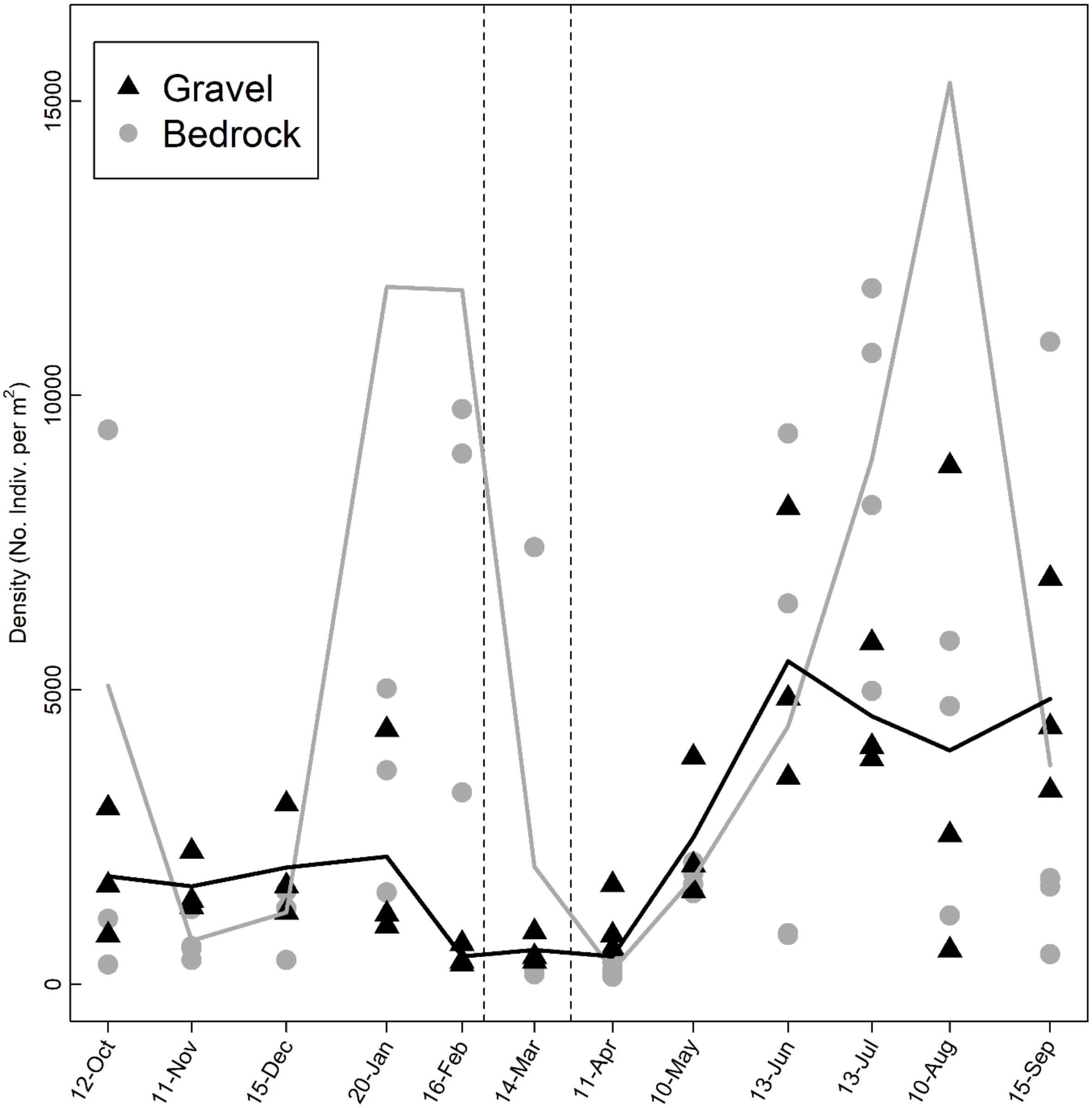

Figure 9. Densities (number of individuals per square meter) of insects through time (ordinal date). Black triangles represent individual Surber samples from the gravel reach. Grey circles indicate individual samples from the bedrock reach. Solid black and grey lines represent means of combined Surber samples for the gravel and bedrock reach, respectively. Vertical dashed lines are plotted at the dates of the two flood events. Three individual bedrock Surber samples from the full year of data with extremely high values are not displayed in order to display more clearly the other points: 20-January (N = 37,155), 16-February (N = 25,122), 10-Aug (N = 49,522).

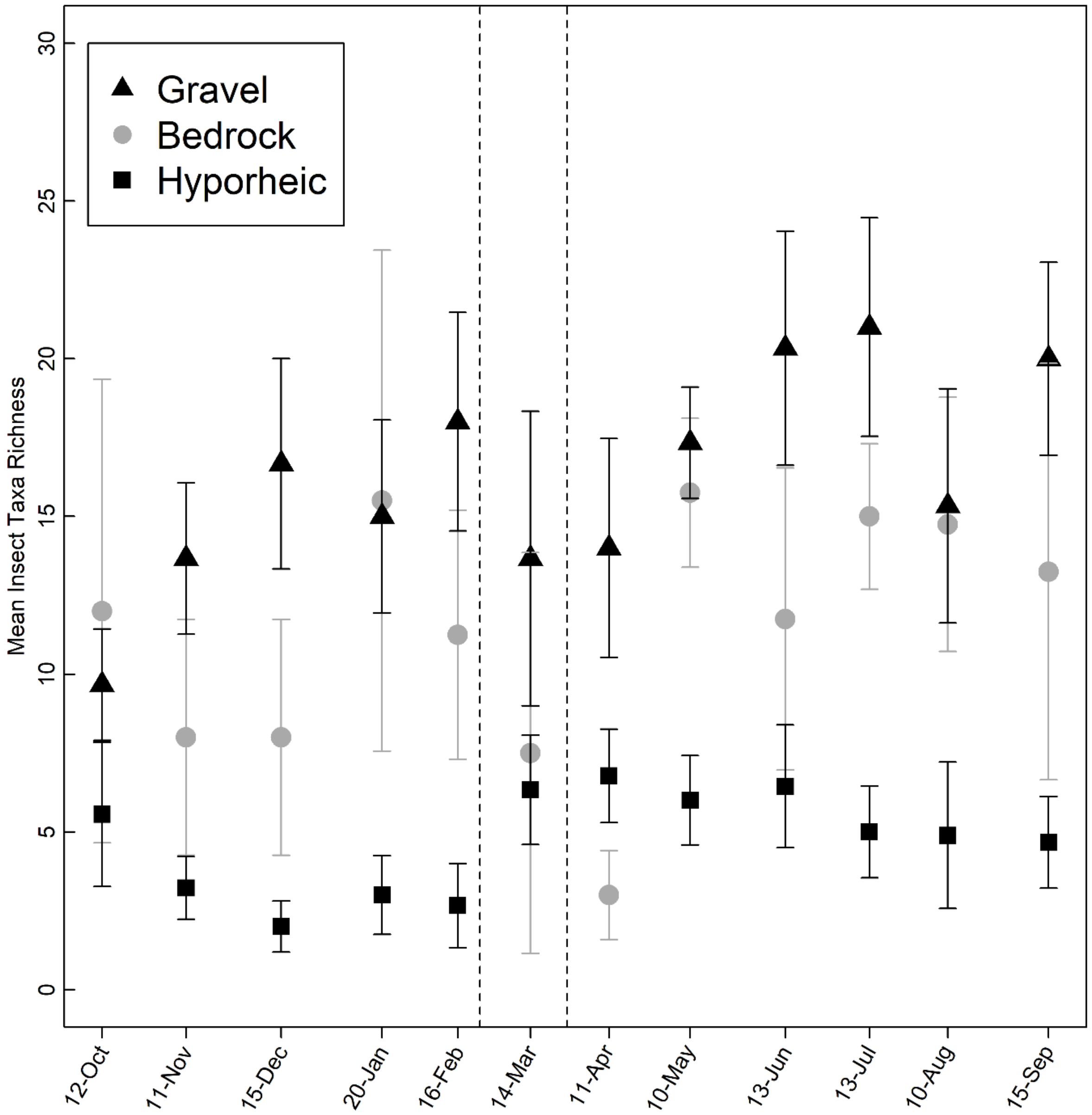

Figure 10. Insect taxa richness through time (ordinal date). Black triangles, grey circles, and black squares are mean richness across samples from the gravel reach, bedrock reach, and hyporheic samples, respectively. Error bars are ± 2 SE. Vertical dashed lines are plotted on the dates of the two flood events.

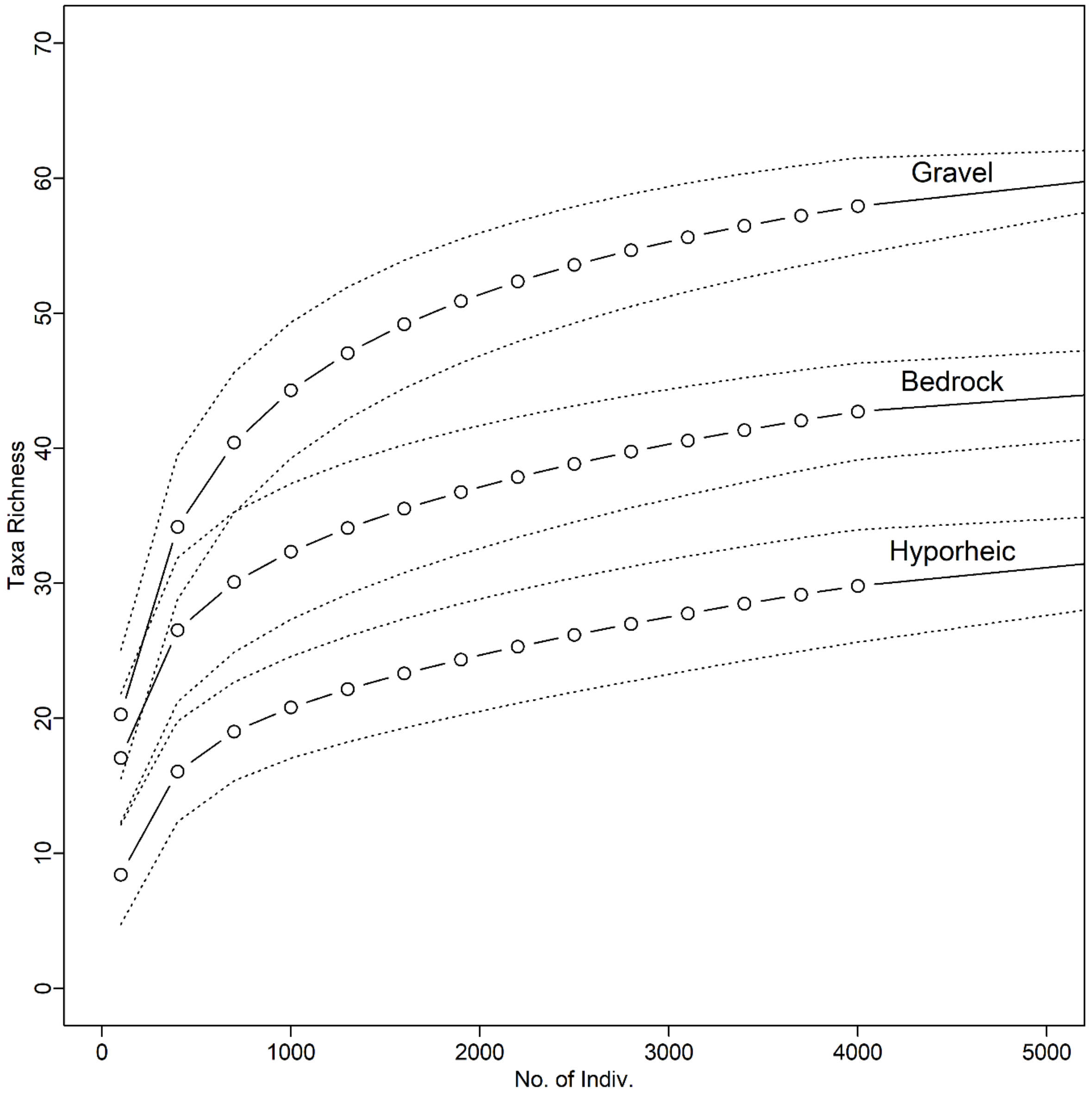

Figure 11. Rarefaction of gravel, bedrock, and hyporheic habitats showing expected taxonomic richness increases as more individuals are sampled. See methods for details. Dotted lines are ± 2 SE.

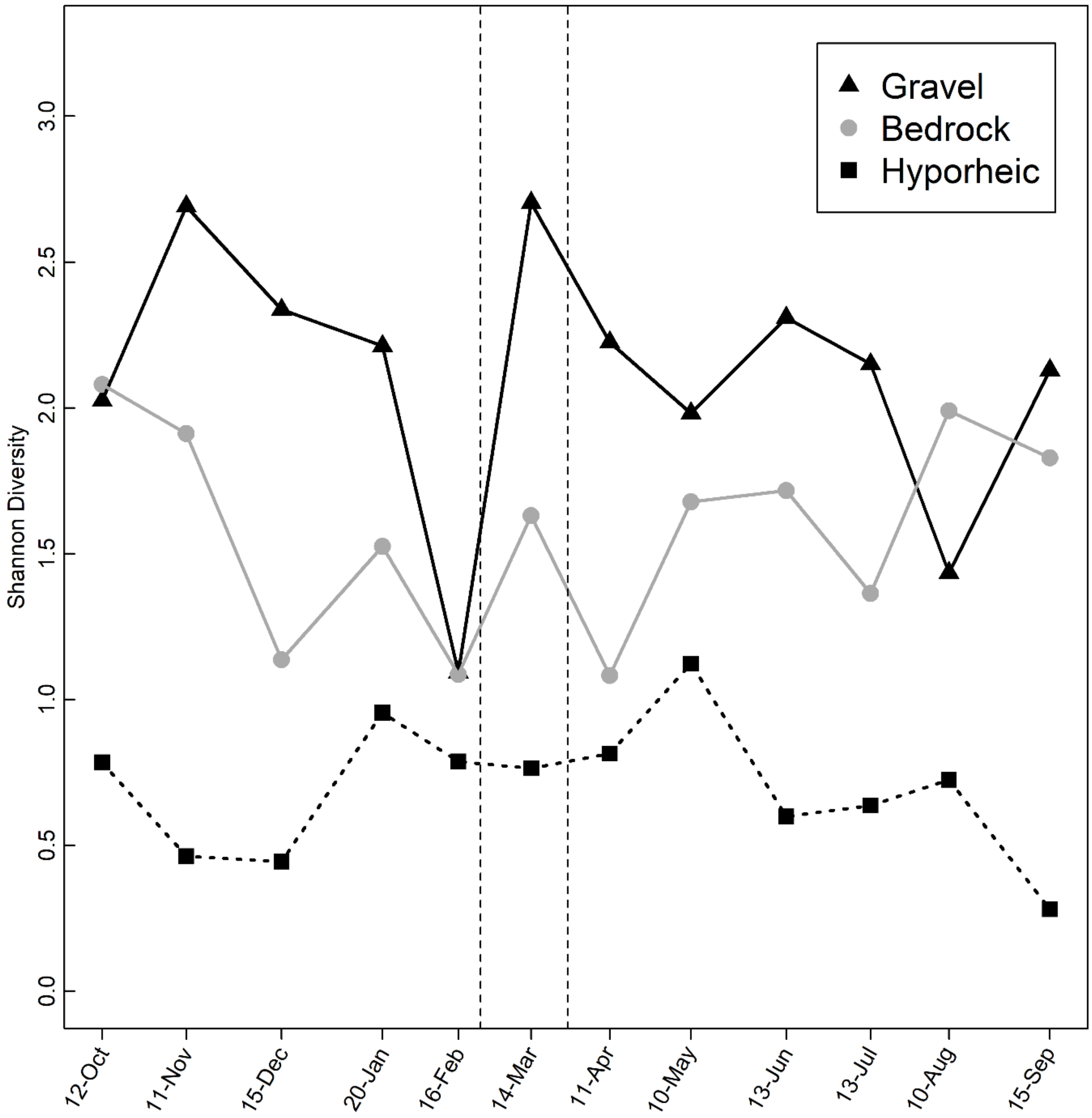

Figure 12. Pooled Shannon diversity through time (ordinal date) for gravel reach (black triangles), bedrock reach (grey circles), and hyporheic habitat (black squares). Vertical dashed lines are plotted at the dates of the two flood events.

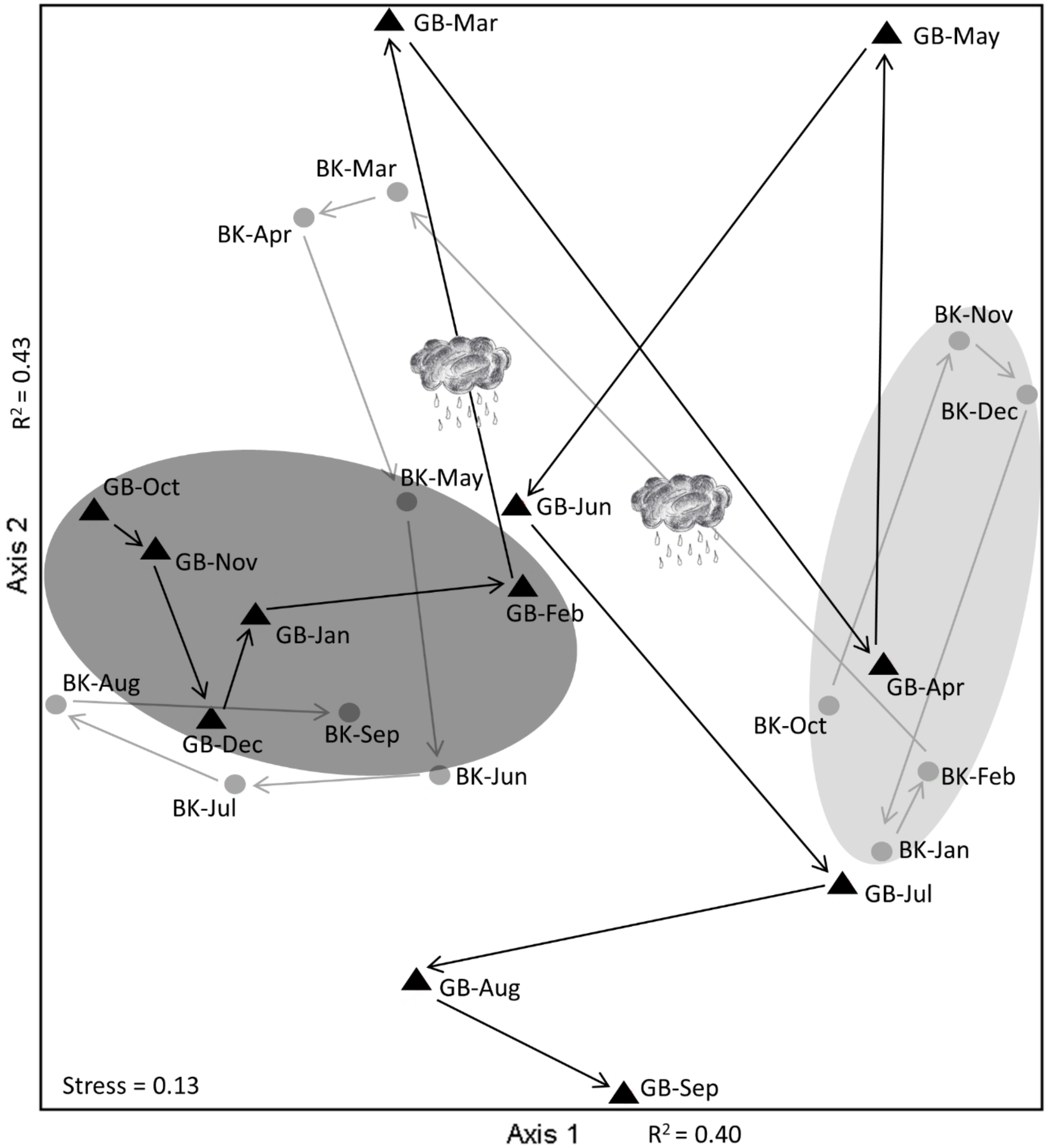

Figure 13. Non-metric multidimensional ordination of the community data labeled with BK=bedrock and GB=gravel and corresponding month of pooled Surber samples. Ellipses shown are outlining approximate space of dry season gravel (dark gray) and bedrock (light gray) communities. Arrows are vectors between sampling dates. Rain clouds indicate when the first flood event (24-Feb) occurred.

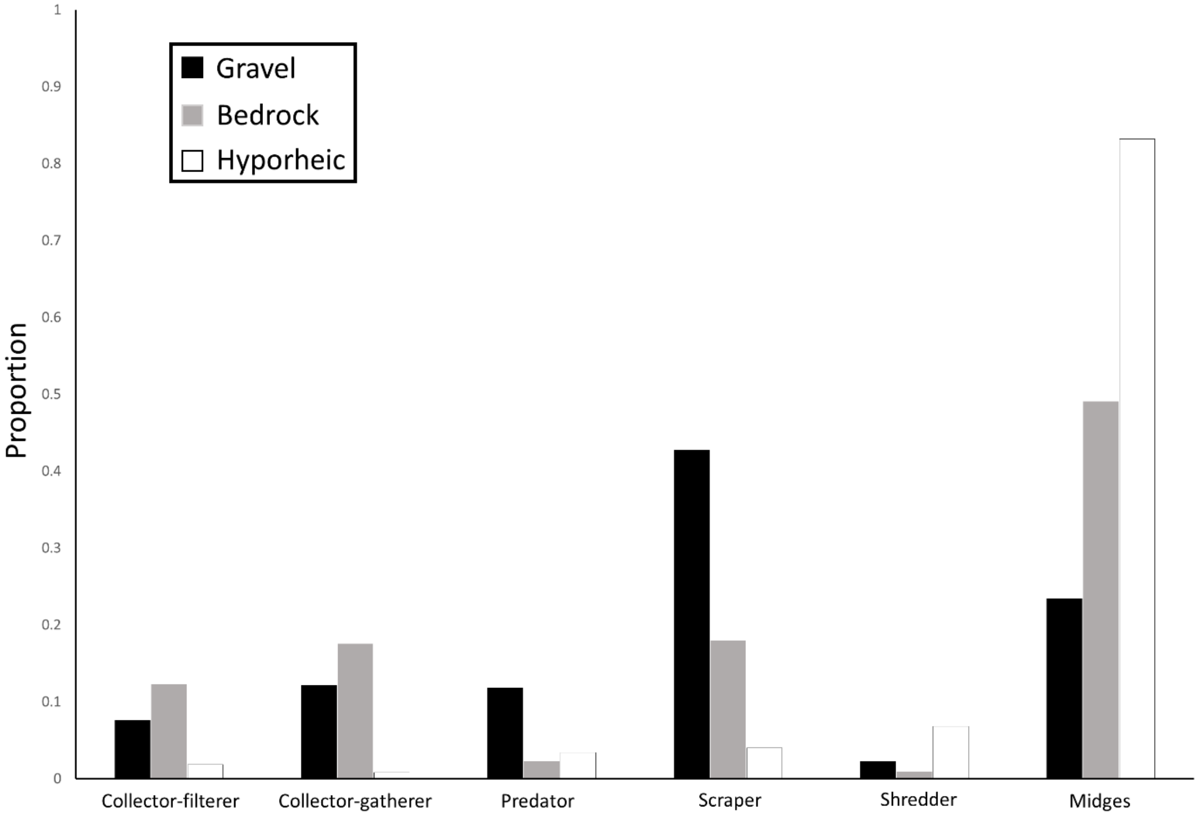

Figure 14. Proportion of insect community in the five major functional feeding groups from gravel (black bar), bedrock (gray bar), and hyporheic samples (white bar) across the entire year of sampling. Midges (Chironomidae) were not included because they were identified only to family level.

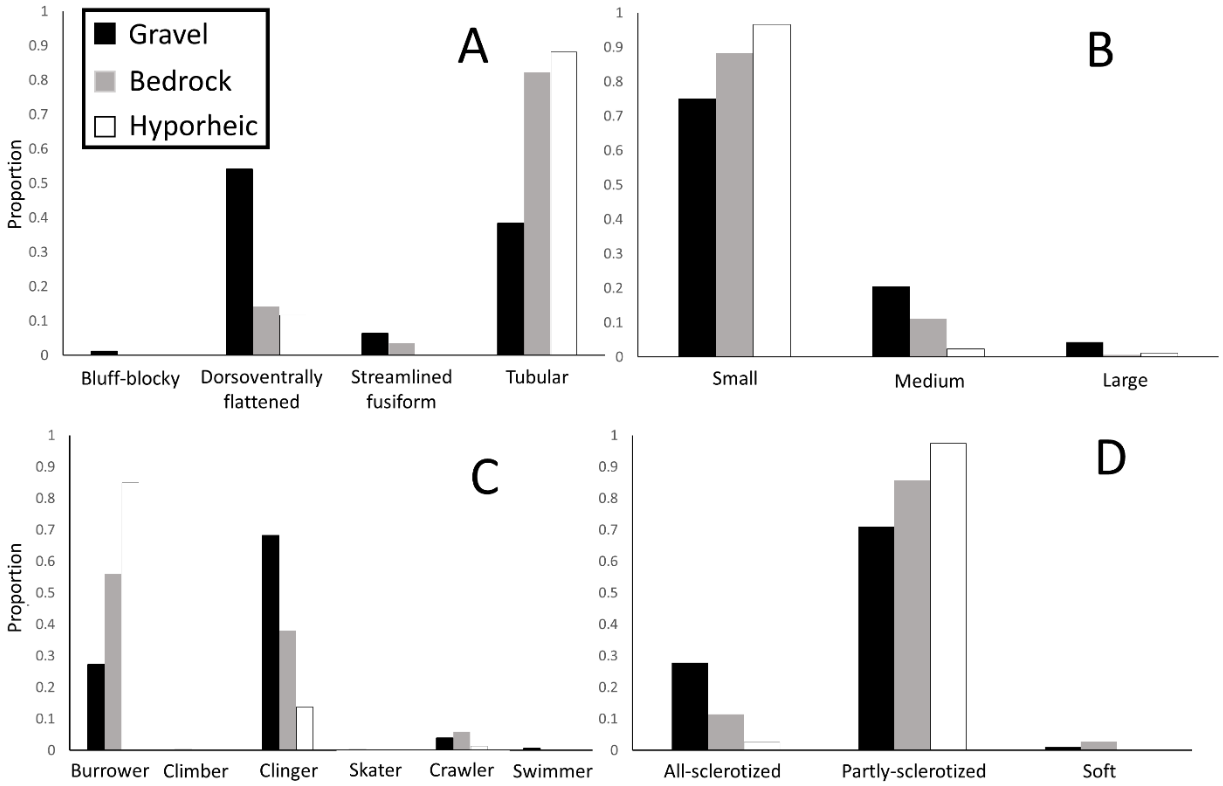

Figure 15. Proportion of insect community broken down by body shape (A), primary habit (B), body size (C), and body armor (D) from gravel (black bars), bedrock (gray bars), and hyporheic habitats (white bars). Data was pooled from the entire year of sampling.

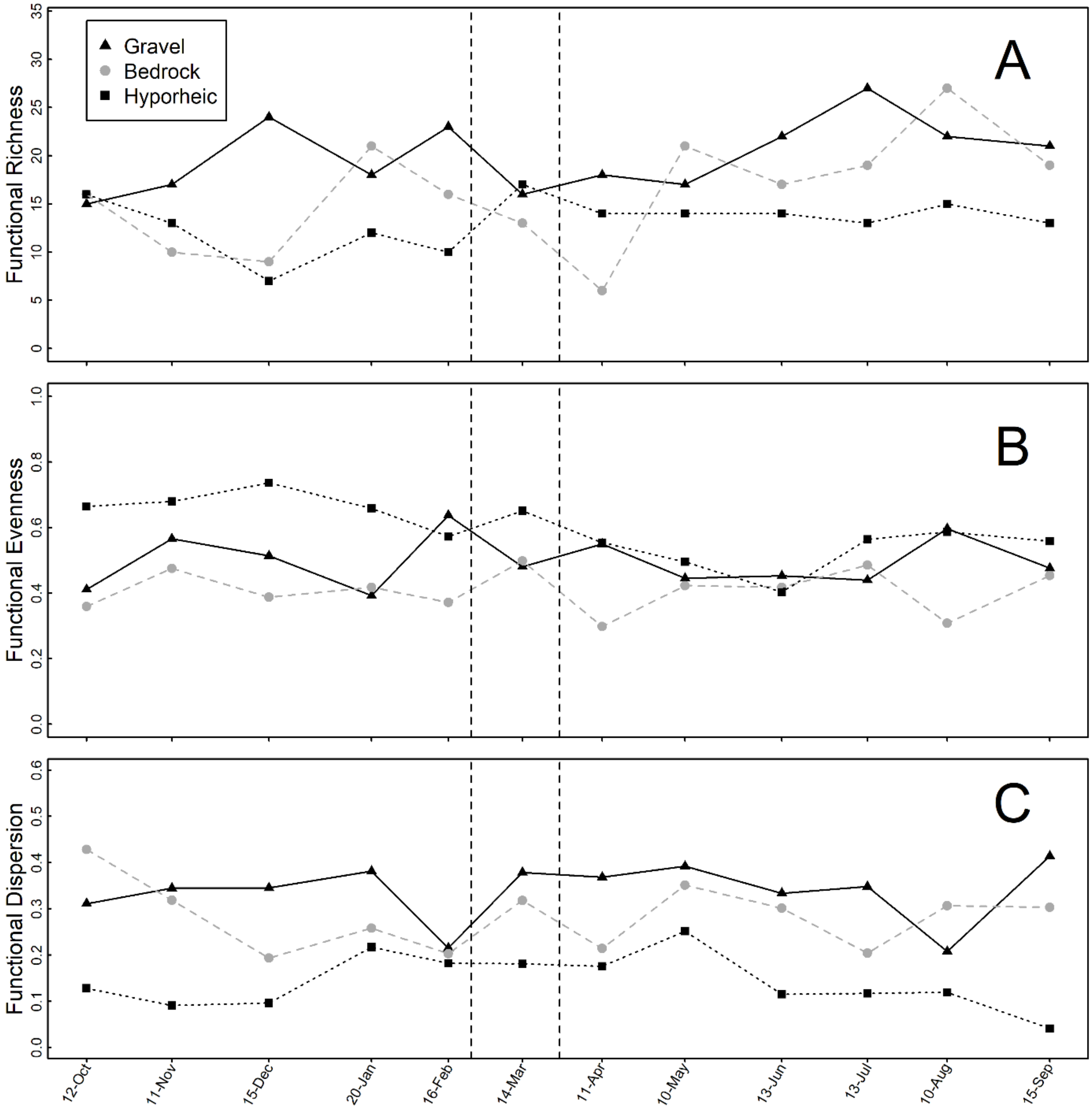

Figure 16. Functional richness (A), functional evenness (B), and functional dispersion (C) of gravel (black triangles), bedrock (grey circles), and hyporheic (black squares) samples through the year.

SUMMARY

The results of my studies reinforce the value of vertical connectivity to stream function. My first chapter demonstrated that hyporheic zones are capable of contributing to instream secondary production. Because I only looked at one of many hyporheic inhabitants, it is likely that the total contribution could be substantial. In the second chapter, I found diversity of benthic insects to be greater in a gravel-bed reach that had more vertical connectivity than a bedrock-lined reach within the same stream. Additionally, the temporal data from the gravel-bed reach suggested that the aquatic insect community was more taxonomically and functionally resilient following two greater than bankfull flood events.

Stream connectivity affects both the stream and terrestrial ecosystems through which streams flow. Longitudinal connectivity of streams links small headwaters to large rivers, flowing from the mountains to the plains and eventually to the ocean (Vannote et al., 1980). Lateral connectivity transports nutrients and biomass from the stream to the floodplain and from the floodplain to the stream, which can subsidize aquatic and terrestrial ecosystems (Hynes, 1975; Nakano & Murakami, 2001). Finally, vertical connectivity joins surface and subsurface habitats, generating a zone of mixing and unique interstitial habitats (Boulton et al., 2010; Stubbington et al., 2016).

Streams are dynamic systems and subject to flow extremes (flooding and drying). The impact of flow disturbance on instream communities is buffered by the three-dimensional connectivity in streams. Habitat heterogeneity along longitudinal paths of stream systems, adult insect avoidance by escaping laterally into the terrestrial environment, and vertical migration into the interstices are just a few of the mechanisms by which connectivity influences aquatic community resistance and resilience to disturbance.

Research into vertical connectivity and the hyporheic zone still lags behind benthic investigations into longitudinal and lateral connectivity (Boulton, 2007). However, with hyporheic zones threatened in many streams by sediment deposition that can clog interstitial spaces and interrupt vertical connectivity, it is essential we understand the possible impacts to invertebrate communities and the greater food web.

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APPENDICES

Appendix A

Pump design and construction

Materials:

1. Simmons® 1160/PM500 No. 2 pitcher pump
2. 1 ¼” to 1 ¼” (3.175 cm) galvanized pipe nipple
3. 1 ¼” to ¾” (1.9 cm) galvanized pipe reducing coupler
4. ¾” to ¾” galvanized pipe nipple (6” or 15.24 cm length, 4.5” or 11.4 cm of its length machined to 1” or 2.5 cm outside diameter)
5. 2” rubber coupler
6. 2 hose clamps
7. Piece of 1” (I.D. 2.5 cm) PVC pipe
8. Amazing GOOP plumbing adhesive
9. Plumbing tape

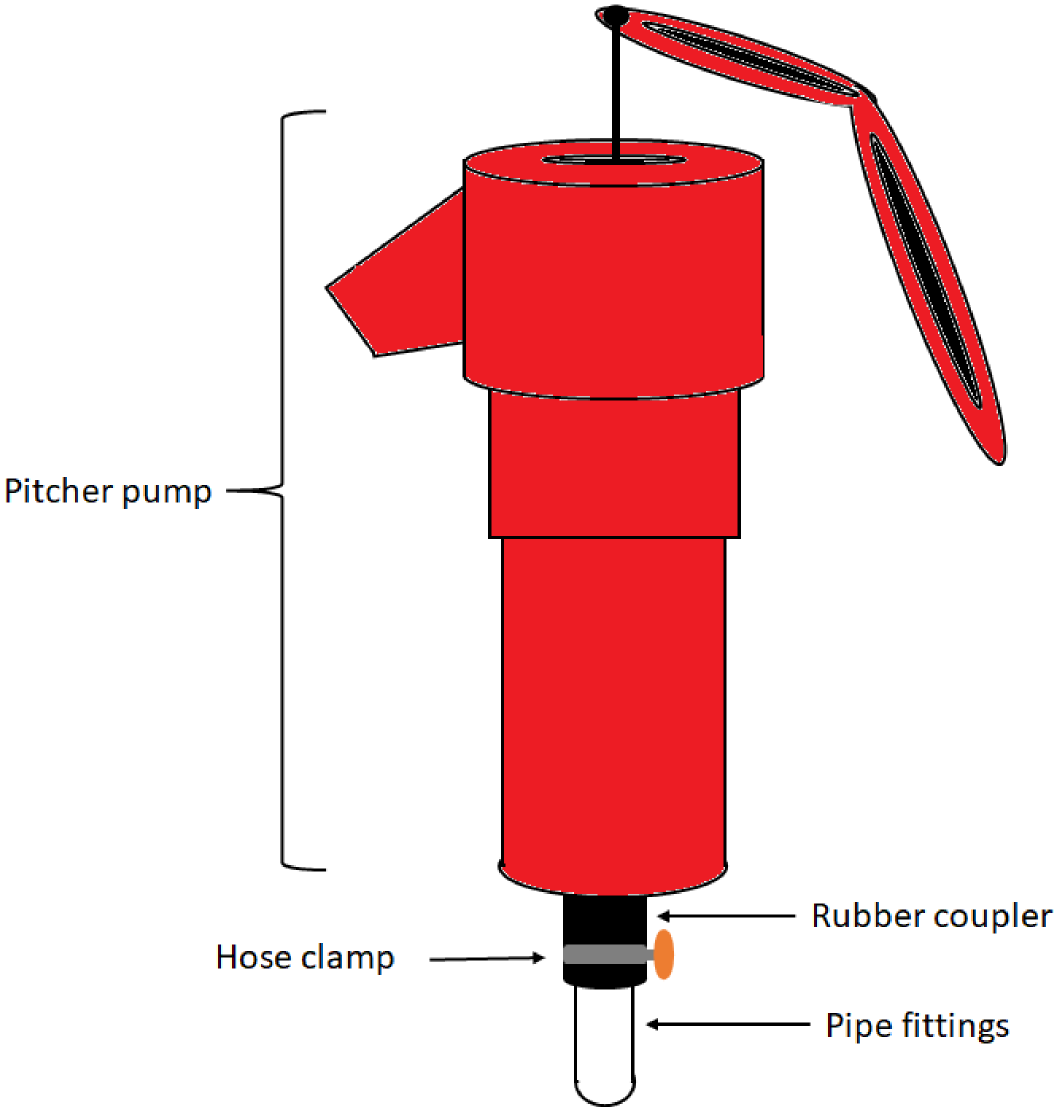
In order to create a pump that could be moved from well to another with ease, I had to construct a coupling system with some readily available pipe fittings (A-1). First, I attached a 1 ¼” to ¾” adapter to the bottom of the pump. The adapter screws on to the bottom of the well with a female end and has another female end on the ¾” side. Before screwing this adapter on to the pump I wrapped the male end coming from the bottom of the well with plumbing tape to make a water tight seal. The fittings are designed so that tape may be unnecessary, but I added the tape just to ensure a tight seal.

The 6” length of ¾” galvanized nipple had to be machined down on one end to fit inside the 1” PVC wells that we were using (A-2). I had access to a machine shop and used a lathe with a carbide insert to machine 4.5” of the nipple down to approximately 1” diameter. Machining 4.5” of the nipple down to this diameter left sufficient room to attach a 1 ½” length of 1” PVC and allowed enough of the nipple to fit inside the wells for a secure hold. Once the ¾” nipple was machined down, I attached a 1 ½” length of 1” SCH40 PVC pipe to the upper portion of the machined end of the nipple using amazing GOOP plumbing adhesive. I wrapped threads of the upper (unmachined) end of this nipple with plumbing tape and screwed it into the adapter that I had attached to the bottom of the pitcher pump.

The rubber coupler was secured to the glued PVC piece using a hose clamp and in such a way as to overhang the machined portion of the galvanized ¾” nipple. On the bottom end of the rubber coupler, I used a hose clamp with a toggle fastener instead of the traditional hex-bolt fastener as it required no additional tool (i.e., could be hand tightened) and was easier to manage in the field. The completed pump with plumbing fittings looked as in A-3.

Appendix A-1. Pipe fittings that make up the coupling system (not to scale). From left to right, the 1 ¼” to 1 ¼” (3.175 cm) galvanized pipe nipple, the 1 ¼” to ¾” (1.9 cm) galvanized pipe reducing coupler, and the 6” (15.24 cm) in length ¾” to ¾” galvanized pipe nipple

Appendix A-2. The nipple after 4.5" (11.4 cm) of its length has been machined down to a 1" (2.5 cm) outside diameter.



Appendix A-3. Diagram of the Bou-Rouch pump with coupling system.

Well driver

Materials:

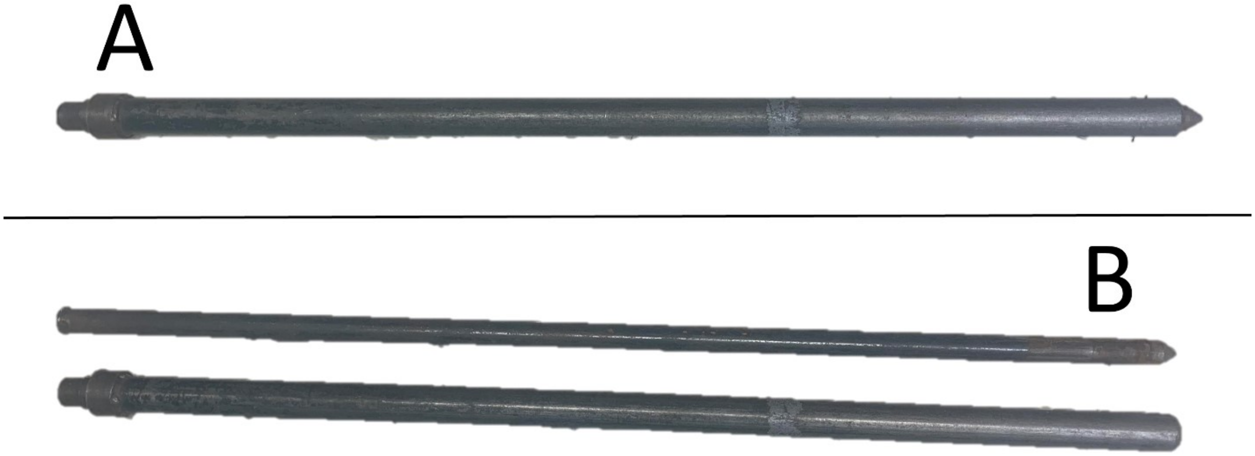
*** The well driver requires a machine shop to construct. ***

1. Steel pipe for tube (1 ½” Schedule 40, black or galvanized steel, O.D. = 4.9 cm, I.D. 3.8 cm)
2. Custom made cap for tube with collar
3. Steel inserts for top and bottom of tube (these prevent some rattling of core)
4. Steel pipe for core (1” Schedule 40, black or galvanized steel, O.D. = 3.3 cm)
5. Custom made tip for core (made to fit O.D. of 1” SCH40 pipe, 3.3 cm)
6. Custom made solid cap for core (made to fit O.D. of 1” SCH40 pipe, 3.3 cm)
7. Chunk of solid steel for cap

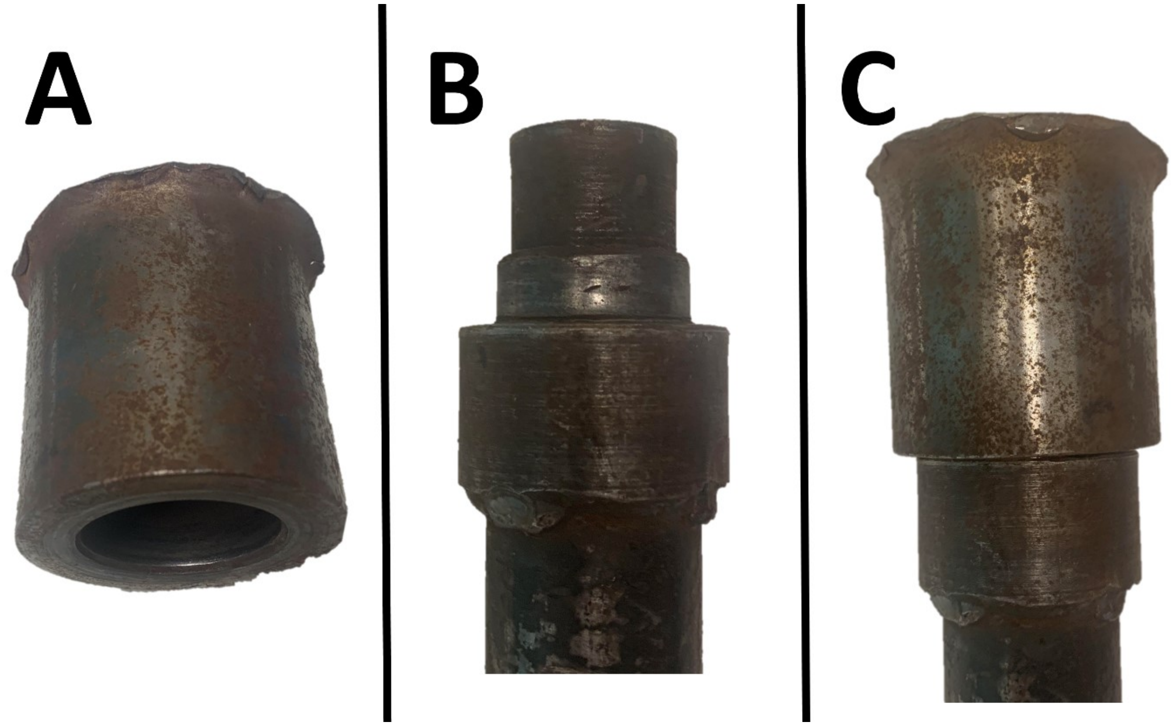
The well driver consists of three main parts: the shell or tube, the inner core, and a cap. The tube (A-4A and B) is made mostly of 1 ½” SCH 40 black steel pipe and is approximately 145 centimeters in total length. The tube has a custom steel cap with collar welded to one end of the tube. The tube is fitted with two approximately 15 cm steel inserts on the inside of the tube at both the top and bottom. These steel inserts have an inside diameter of approximately 3.5 cm and make the I.D. of the tube at both ends closer to the O.D. of the inner core. The steel inserts simply prevent some rattling of the core when it is inserted.

The inner core (A-4B) is made mostly of 1” SCH 40 black steel pipe and is approximately 3 cm longer than the tube (148 cm total length) and has two custom parts welded to each end. A cap is welded to the top of the inner core that is approximately 5 cm in length and is machined down to match the outside diameter of the 1” SCH 40 steel pipe. At the other end of the core (the tip) is another custom piece of steel that is approximately 15 cm in length and is also machined down to match the O.D. of the steel pipe. One end of this tip is ground down to form a point that is approximately 2 cm long.

The cap (A-5A) is made from solid steel. A hole is initially drilled in one side of the chunk of steel and gradually widened. Care should be taken not to drill too deeply. I left approximately 2.5 cm at the top of the cap because most of the force from driving is being absorbed there. The wall thickness is not entirely critical but should at least match the O.D. of the collar created for the tube (A-5B). You can see in A-5C that the cap was actually quite a bit larger than the collar on the tube. The I.D. of the cap is more critical and should closely match the O.D. of the top portion of the tube (pictured in A-5B just above the collar).



Appendix A-4. The core inserted into the tube of the well driver (A). The core removed from the tube (B).



Appendix A-5. The cap (A), the collar of the tube (B), and the cap placed on top of the tube (C).

Well construction and installation

Materials:

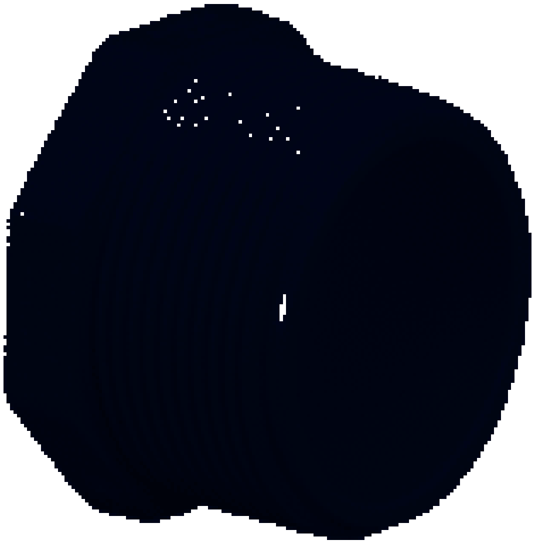
1. 1” (ID: 2.5 cm) SCH40 polyvinyl chloride (PVC)
2. PVC plugs
3. 5 mm drill bit
4. Drill
5. PVC cutters
6. Plumbing (PVC) sealant

Needed for installation:

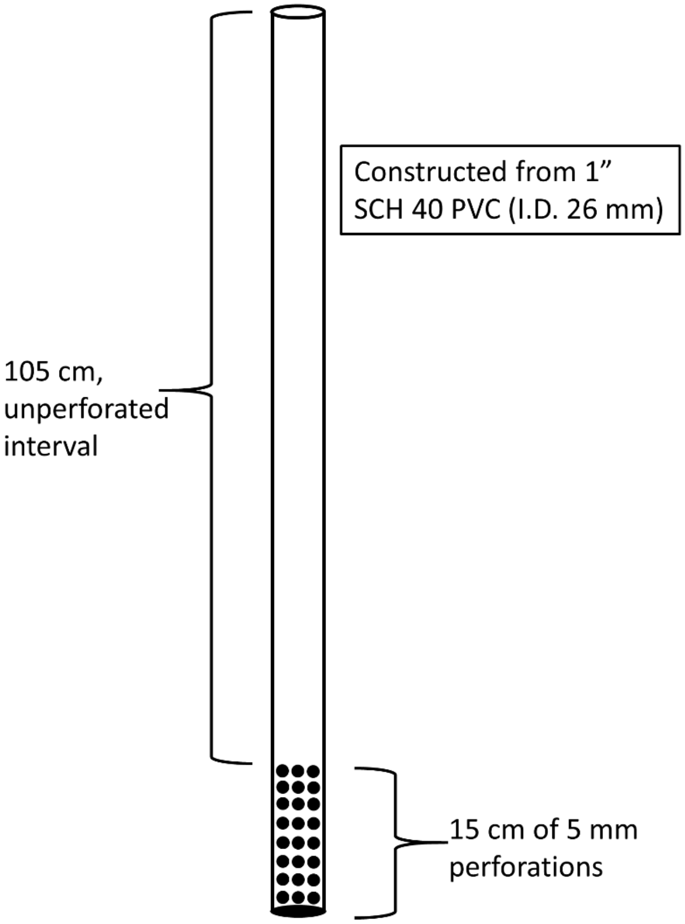
1. Well driver and cap
2. Gloves
3. Sledge hammer

I constructed hyporheic wells using polyvinyl chloride (PVC) pipe (SCH40, ID: 2.5cm) that were similar in design to those used by Hunt and Stanley (2000). I cut PVC pipe to a total length of 120 cm and sealed one end of the pipe with a PVC plug and PVC sealant. The PVC plug can be purchased (A-6) or created using a sheet of plastic and a punch. The plugs need to have an outside diameter that fits in to one side of the well (1”). The purpose of the plug is simply to seal the screened end of the wells, so how this is accomplished is largely unimportant. If purchasing the plugs, it may be helpful to take a piece of the 1” SCD 40 PVC with you to ensure that the plug will fit inside the wells.

I created a 15 cm screen in the closed end of the pipe composed of many (approximately 45) 5 mm perforations (A7). I installed wells using a steel driver so that the screen was at approximately 30-45 cm depth below gravel surface. Hammer the well driver down to the appropriate depth, remove the inner core, insert the PVC well, and remove the outer shell of the well driver. Take care when removing the shell of the well driver so that the well does not move up. It may be helpful to mark wells at the appropriate depth before installation so that once installed you can ensure they are at the correct sampling depth. You can use the core of the well driver to hold the PVC well in place. I would caution against using force on the PVC well to try to get it to stay down as this has a tendency to disturb the substrate and lodge fine sediment between the PVC well and the shell of the well driver. Forcing the well down cements the well inside the driver and may result in having to re-drive the well.



Appendix A-6. Threaded PVC plug that can be purchased from a hardware store and inserted into the screened end of the wells to seal the bottom.



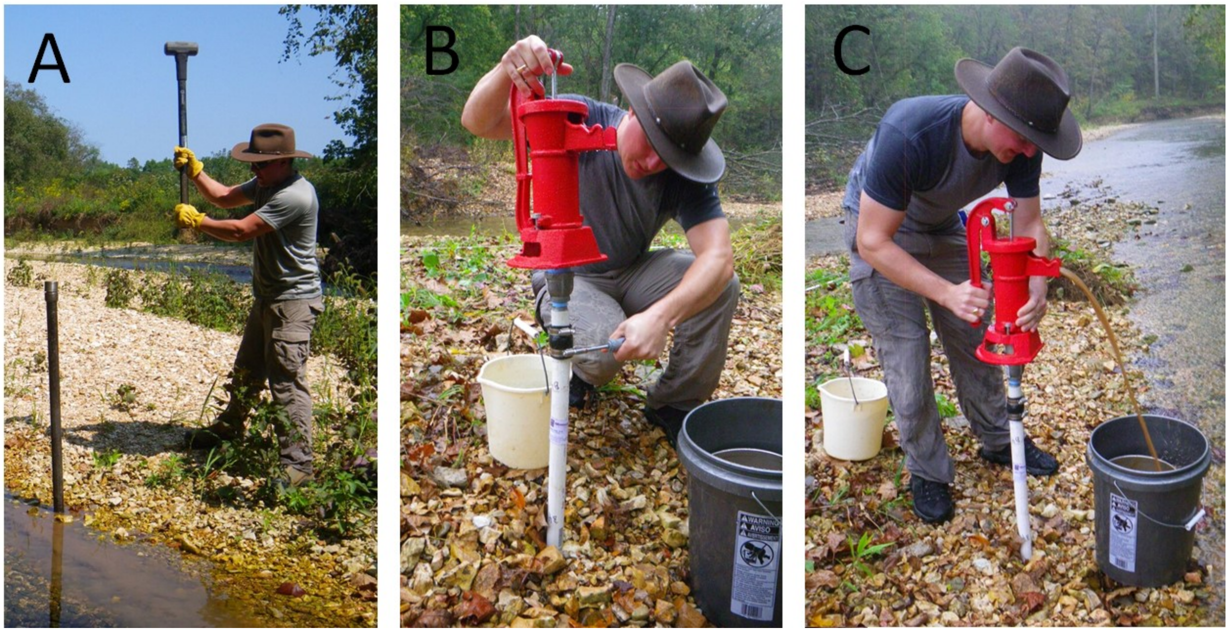
Appendix A-7. General well design. Each well was constructed from PVC and plugged at the screen end. The screen consisted of 15cm of 5mm perforations.

The pumping procedure

Materials:

1. Pump with coupler attached
2. Installed hyporheic wells
3. 1 L primer bottle
4. 5-gallon (19 L) bucket with 9 L fill line marked on the inside
5. Sieve
6. Two squirt bottles (water & ethanol)
7. Funnel
8. Sample containers
9. 95% ethanol for sample storage

Upon arriving at the sampling site, the pump should be submerged in water for approximately 15 minutes. The valves inside pump are made from leather and require soaking so that they can swell up and form a tight seal. While the pump is soaking, prep for pumping of the well by filling the 1 L primer bottle and the squirt bottle with filtered stream water. You can use the sieve to filter the water as you fill the bottles. Start sampling with the most downstream well and work upstream. To pump the wells, insert the machined galvanized coupler at the base of the pump into the well and tighten the bottom hose clamp to the well (A-8). Once the pump is attached, place the handle of the bucket on the spout of the pump. Lift the handle of the pump and pour the liter of filtered stream water into the top of the pump. You can begin pumping after approximately half of the water is in the pump. If you do not use the entire liter of priming water, pour the remainder into the bucket. The goal is to collect 8 L of hyporheic water and the fill line that is pre-marked on the bucket is 9 L (8 L plus the 1 L of filtered stream water). Continue to pump at a constant rate (approximately 16 liters per minute) until the full sample is collected. Once the water reaches the 9 L mark, stop pumping, remove the bucket, and pour the water through the sieve to separate out sediment and invertebrates. Use the squirt bottle with filtered stream water to move all the sediment and invertebrates to one side of the sieve. Use the ethanol squirt bottle and the funnel to wash sediment and invertebrates into a sample container. Ensure that an appropriate label has been placed in the sample container before sealing. Once a sample is collected, remove the pump and submerge in the water. Pump the handle of the pump while it is submerged to clear the pump of any debris before moving to the next well. Repeat the pumping process until all samples are collected.



Appendix A-8. Panels showing the well installation (A), attaching the pump (B), and pumping the well (C).

Appendix B

Tables of taxa collected in the benthic (Table B1 and Table B2) and hyporheic zones (Table B3) by month from Bull Creek. Abundance data is presented as a mean per sample unit. For benthic samples in the gravel bar mean abundances are from three Surber samples, for benthic bedrock samples mean abundances are from four Surber samples and for hyporheic samples mean abundances are from nine hyporheic well pumps (8 L each), except in August when only 7 wells were pumped. Taxa list is for mostly immature stages of aquatic insects.

Table B1. Taxa list with mean abundances (per Surber sample) from the gravel-bedded reach of Bull Creek.

	GBOct17	GBNov17	GBDec17	GBJan18	GBFeb18	GBMar18	GBApr18	GBMay18	GBJun18	GBJul18	GBAug18	GBSep18
COLEOPTERA												
Dubiraphia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Microcylloepus	0.00	0.33	0.33	0.00	0.33	0.00	0.00	0.00	0.33	0.00	0.33	0.00
Optioservus	2.67	6.00	39.00	13.67	14.67	2.00	1.67	6.67	12.33	15.33	6.33	10.67
Stenelmis	0.33	1.67	0.33	0.00	0.00	0.33	0.67	0.33	1.67	1.33	0.67	4.67
Lutrochus	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.33
Hydrochus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ectopria	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.33	0.33	0.00
Psephenus	21.33	7.67	31.67	4.00	3.33	1.00	0.67	16.33	26.33	128.33	203.33	111.67
DIPTERA												
Atherix	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	1.00	1.00	0.00	0.00
Bezzia/Palpomyia	0.00	0.00	0.67	4.00	1.33	0.00	0.33	0.00	0.33	0.67	0.00	0.00
Forcipomyia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Probezzia	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chironomidae	3.00	3.00	15.00	54.00	215.67	9.67	16.67	99.67	79.67	12.00	3.67	103.67
Corethrella	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Anopheles	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hemerodromia	0.00	0.33	0.67	0.00	2.00	0.00	0.00	0.00	2.00	0.00	0.00	0.33
Trichoclinocera	0.00	0.00	0.00	0.00	0.00	0.00	0.67	0.00	0.00	0.00	0.00	0.00
Caloparyphus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Tabanus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.67
Antocha	0.00	0.00	0.00	0.00	2.33	0.00	0.00	0.00	0.00	1.33	0.00	0.00
Hexatoma	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.33	1.33	0.33	0.33
Tipula	0.00	0.67	0.00	0.33	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Simulium	0.00	0.00	0.00	0.33	0.33	0.00	0.00	0.33	0.00	0.00	0.00	0.67
Prosimulium	0.00	0.00	0.00	0.00	0.00	0.67	0.00	5.00	0.00	0.00	0.00	0.00
EPHEMEROPTERA												
Acentrella	0.33	0.00	0.00	0.00	3.33	4.33	3.00	15.00	2.00	0.00	0.00	3.33

Acerpenna	0.33	0.00	0.00	0.00	0.33	0.00	1.00	0.67	1.33	0.00	0.00	3.33
Baetis	1.00	0.33	0.67	0.00	0.33	0.00	3.67	17.67	60.67	97.33	0.67	50.67
Paracloedes	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Caenis	1.33	0.00	1.67	0.33	1.67	0.33	0.00	0.00	24.67	2.00	1.00	5.33
Ephemera	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Attenella	0.00	1.67	3.67	1.67	2.33	0.67	0.67	0.00	0.00	0.00	0.00	0.00
Dannella	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ephemerella	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Maccaffertium	12.67	11.33	6.00	15.00	4.33	1.67	0.67	3.67	12.00	7.00	1.67	4.33
Stenacron	0.00	0.00	3.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.33	1.00
Stenonema	0.67	5.33	4.00	7.33	5.67	4.67	19.00	18.67	45.33	13.00	19.67	27.67
Isonychia	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.33	0.67	0.00	4.67
Tricorythodes	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	87.00	6.33	0.67	1.00
Choroterpes	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Leptophlebia	0.00	0.00	1.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Paraleptophlebia	0.00	0.00	0.00	0.00	0.00	1.00	1.33	0.00	0.33	0.00	2.33	0.00
HEMIPTERA												
Microvelia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rhagovelia	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	1.33	0.00
LEPTIDOPTERA												
Petrophila	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.67	0.00	0.00
MEGALOPTERA												
Corydalus	0.33	0.00	0.00	0.00	0.00	0.33	0.00	0.33	1.00	11.00	0.67	0.33
Sialis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ODONATA												
Basiaeschna	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Argia	0.00	0.33	2.00	0.33	0.00	0.00	0.00	0.00	0.00	0.67	5.67	0.00
Gomphus	3.67	1.00	9.00	2.67	0.00	0.00	1.33	0.33	0.33	10.00	14.33	27.00
Hagenius	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
PLECOPTERA												
Paracapnia	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Alloperla	0.00	0.00	0.67	0.33	0.00	3.00	3.67	2.00	0.00	0.00	0.00	0.00
Haploperla	0.00	0.00	0.00	0.00	0.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Leuctra	0.00	0.00	0.00	0.00	0.00	0.00	0.67	2.33	0.33	6.33	3.33	2.00
Zealeuctra	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00
Amphinemura	0.00	0.00	0.00	0.00	1.33	1.33	0.67	0.67	0.00	0.00	0.00	0.00
Prostoia	0.00	0.00	0.00	0.33	1.00	1.33	0.00	0.00	0.00	0.00	0.00	0.00
Neoperla	1.33	2.33	2.67	4.67	0.33	3.33	0.00	0.67	1.00	4.33	1.33	3.33
Acroneuria	0.67	1.33	1.67	3.33	1.33	0.33	0.00	0.67	1.67	5.67	3.67	1.67
Perlesta	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.67	3.33	0.00	0.00	0.00
Isoperla	0.00	0.00	0.00	0.00	0.00	1.00	19.33	2.33	0.00	0.00	0.00	0.00
Pteronarcys	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.67	0.00	0.00	0.00	0.00
TRICHOPTERA												
Micrasema	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Glossosoma	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Protoptila	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00
Helicopsyche	7.67	5.33	6.00	6.00	0.33	1.67	0.00	0.67	3.67	13.00	29.67	13.33
Ceratopsyche	0.00	0.33	0.00	0.00	0.00	0.33	0.00	0.00	3.67	0.00	0.00	0.00
Cheumatopsyche	0.67	8.67	0.00	1.33	2.33	2.33	1.67	1.00	35.33	5.67	1.00	5.33
Hydropsyche	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00
Hydroptila	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ochrotrichia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.33	0.00	0.00	0.00	0.00
Mystacides	0.00	1.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00
Oecetis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00
Lepidostoma	0.00	0.00	0.33	2.00	2.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pycnopsyche	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Marilia	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.33	0.00	0.00
Chimarra	0.00	3.67	0.00	0.00	0.00	0.33	0.67	0.00	0.67	3.00	0.00	1.67
Polycentropus	0.00	2.00	2.67	12.33	1.33	0.00	0.33	0.00	0.00	1.00	0.67	0.33
Psychomyia	0.00	0.33	2.67	0.00	1.33	0.33	0.00	0.00	1.00	2.00	0.00	0.00

Table B2. Taxa list with mean abundances (per Surber sample) from the bedrock-lined reach of Bull Creek.

	BKOct17	BKNov17	BKDec17	BKJan18	BKFeb18	BKMar18	BKApr18	BKMay18	BKJun18	BKJul18	BKAug18	BKSep18
COLEOPTERA												
Dubiraphia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.75
Microcylloepus	0.00	0.00	0.00	56.50	91.00	51.25	0.00	0.25	20.75	0.00	71.75	33.25
Optioservus	0.25	0.00	0.25	45.50	23.50	6.00	0.00	2.50	3.50	1.75	20.75	7.25
Stenelmis	0.50	0.00	0.00	4.25	0.00	0.25	0.00	0.25	1.25	2.00	14.00	3.75
Lutrochus	0.25	0.00	0.00	3.75	0.50	2.00	0.25	0.75	1.25	0.00	15.00	5.50
Hydrochus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00
Ectopria	0.00	0.00	0.00	1.25	0.00	0.50	0.00	0.00	0.00	0.25	0.50	0.25
Psephenus	68.25	0.00	0.25	0.25	0.50	0.00	0.00	1.50	0.75	74.00	17.50	8.25
DIPTERA												
Atherix	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00	3.25	1.00	28.00	1.25
Bezzia/Palpomyia	0.00	0.00	0.00	2.50	0.00	0.00	0.00	0.00	0.00	1.00	10.00	0.00
Forcipomyia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00
Probezzia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chironomidae	25.00	15.25	68.25	552.25	746.75	78.75	13.25	92.00	197.00	79.50	380.75	151.50
Corethrella	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Anopheles	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hemerodromia	2.00	0.00	0.25	17.25	11.75	4.25	0.00	0.25	1.50	0.50	5.75	0.50
Trichoclinocera	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Caloparyphus	0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00
Tabanus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00
Antocha	1.50	4.25	2.50	16.25	12.50	0.25	0.00	0.00	3.75	0.00	0.25	0.00
Hexatoma	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Tipula	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Simulium	9.00	1.75	4.25	0.50	4.25	0.25	0.25	0.50	14.75	0.00	0.00	0.50
Prosimulium	12.75	0.00	0.00	0.50	0.00	0.00	0.00	0.00	2.75	0.00	0.00	0.00
EPHEMEROPTERA												
Acentrella	23.50	4.25	6.50	9.00	8.00	2.00	2.00	4.25	0.00	0.00	0.00	1.00

Acerpenna	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Baetis	40.25	0.75	0.50	2.00	0.00	0.00	0.00	3.25	64.00	2.50	2.25	17.25
Paracloedes	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Caenis	0.50	0.25	0.50	15.25	14.00	0.25	0.25	1.25	2.50	22.75	38.50	7.75
Ephemera	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00
Attenella	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.00	0.00
Dannella	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00
Ephemerella	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Maccaffertium	0.00	0.25	0.00	0.00	0.00	0.00	0.00	4.00	0.25	1.50	0.00	0.00
Stenacron	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Stenonema	0.25	0.00	0.00	1.25	0.00	0.00	0.00	18.75	0.50	4.75	0.50	1.50
Isonychia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Tricorythodes	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	18.75	62.25	62.75	1.00
Choroterpes	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Leptophlebia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00
Paraleptophlebia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.50	0.00	0.00	1.50	0.00
HEMIPTERA												
Microvelia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00
Rhagovelia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00
LEPTIDOPTERA												
Petrophila	6.75	0.25	0.00	2.50	2.00	0.00	0.00	0.00	0.25	0.25	0.00	0.75
MEGALOPTERA												
Corydalus	1.25	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00	1.50	0.00	0.00
Sialis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
ODONATA												
Basiaeschna	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00
Argia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00
Gomphus	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.25	0.25
Hagenius	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
PLECOPTERA												
Paracapnia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Alloperla	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00
Haploperla	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Leuctra	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.25	0.00	0.00	0.00	0.00
Zealeuctra	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Amphinemura	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00
Prostoia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Neoperla	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Acroneuria	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00
Perlesta	0.00	0.00	0.00	0.00	0.00	0.00	0.00	10.50	0.00	0.00	0.00	0.00
Isoperla	0.00	0.00	0.00	0.00	1.00	0.00	0.25	0.50	0.00	0.00	0.00	0.00
Pteronarcys	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
TRICHOPTERA												
Micrasema	0.00	0.00	0.00	1.50	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00
Glossosoma	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Protoptila	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Helicopsyche	2.25	4.75	0.50	2.75	19.25	7.00	3.50	1.25	2.50	391.00	176.25	22.75
Ceratopsyche	17.00	0.00	5.00	10.00	1.25	0.25	0.00	0.00	4.25	0.00	0.00	0.00
Cheumatopsyche	2.50	2.00	0.50	43.25	18.25	2.50	0.00	0.75	2.75	0.50	8.00	2.25
Hydropsyche	88.25	15.50	3.00	54.50	6.50	10.25	0.00	0.00	8.50	0.00	4.00	7.50
Hydroptila	0.00	0.00	0.00	3.50	3.00	1.00	0.00	0.00	1.25	0.25	8.00	2.00
Ochrotrichia	0.00	0.00	0.00	0.00	4.00	0.00	0.00	2.75	0.00	0.00	0.00	0.00
Mystacides	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.00
Oecetis	0.00	0.00	0.00	0.50	0.50	0.00	0.00	0.50	0.00	2.50	2.25	1.00
Lepidostoma	0.00	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pycnopsyche	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Marilia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00
Chimarra	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.25	0.00	0.00	0.00	0.00
Polycentropus	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Psychomyia	1.75	3.25	1.25	4.50	9.50	4.00	0.00	0.75	5.50	0.50	0.25	0.25

Table B3. Taxa list with mean abundances (per 8 L pump sample) from the hyporheic zone in the gravel-bedded reach of Bull Creek.

	HZOct17	HZNov17	HZDec17	HZJan18	HZFeb18	HZMar18	HZApr18	HZMay18	HZJun18	HZJul18	HZAug18	HZSep18
COLEOPTERA												
Dubiraphia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Microcylloepus	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Optioservus	0.44	0.00	0.00	0.11	0.00	0.00	0.67	0.67	0.44	0.00	0.00	0.00
Stenelmis	0.56	0.11	0.00	0.11	0.00	0.22	0.89	0.00	0.44	0.22	0.67	1.00
Lutrochus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hydrochus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ectopria	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Psephenus	0.56	1.56	0.56	0.56	0.11	0.44	1.33	1.22	0.00	0.11	0.00	0.11
DIPTERA												
Atherix	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Bezzia/Palpomyia	0.78	0.22	0.11	0.11	0.00	0.00	1.44	0.67	0.00	0.00	0.33	0.56
Forcipomyia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.22	0.00	0.00
Probezzia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chironomidae	47.00	56.44	16.00	13.22	13.33	112.22	87.67	38.44	204.00	161.67	105.00	173.67
Corethrella	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.11	0.00	1.22	2.78	0.78
Anopheles	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hemerodromia	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Trichoclinocera	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Caloparyphus	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.00
Tabanus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Antocha	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hexatoma	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Tipula	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Simulium	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.00	0.00	0.00
Prosimulium	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
EPHEMEROPTERA												

Acentrella	0.00	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Acerpenna	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Baetis	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.11
Paracloedes	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Caenis	0.11	0.11	0.00	0.00	0.00	0.56	0.11	0.11	5.22	0.00	0.67	0.00
Ephemera	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Attenella	0.22	0.00	0.00	0.11	0.11	0.11	0.00	0.00	0.00	0.00	0.00	0.00
Dannella	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ephemerella	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Maccaffertium	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.11	0.00	0.00	0.00
Stenacron	0.00	0.00	0.00	0.00	0.00	0.78	0.22	0.11	0.00	0.00	0.00	0.00
Stenonema	0.56	0.44	0.22	0.89	0.89	2.11	0.22	0.67	0.44	0.44	1.00	1.44
Isonychia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Tricorythodes	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.22	0.00	0.00	0.00
Choroterpes	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.00	0.00	0.00
Leptophlebia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.22	0.00	0.00	0.00
Paraleptophlebia	0.22	0.00	0.00	0.00	0.11	0.11	0.56	1.67	1.44	1.11	0.56	0.00
HEMIPTERA												
Microvelia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rhagovelia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
LEPTIDOPTERA												
Petrophila	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MEGALOPTERA												
Corydalus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sialis	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.11	0.00
ODONATA												
Basiaeschna	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Argia	0.44	0.56	0.00	0.44	0.00	0.22	0.44	0.11	0.22	0.33	0.67	0.11
Gomphus	0.22	0.11	0.00	0.22	0.22	0.78	0.44	0.33	0.22	1.11	1.44	0.44
Hagenius	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
PLECOPTERA												

Paracapnia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Alloperla	0.00	0.00	0.00	0.11	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00
Haploperla	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Leuctra	0.00	0.00	0.00	0.00	0.78	16.22	11.56	8.89	11.78	7.00	1.67	0.33
Zealeuctra	0.33	0.33	0.22	0.11	0.11	0.00	0.22	0.00	0.00	0.00	0.00	0.00
Amphinemura	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Prostoia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Neoperla	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.22	0.00
Acroneuria	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Perlesta	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Isoperla	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pteronarcys	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.00
TRICHOPTERA												
Micrasema	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00
Glossosoma	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Protoptila	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Helicopsyche	0.67	0.11	0.11	0.00	0.00	1.56	0.44	0.44	0.11	1.33	0.56	0.11
Ceratopsyche	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cheumatopsyche	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.22	0.00	0.00	0.00
Hydropsyche	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hydroptila	0.00	0.00	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ochrotrichia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mystacides	0.00	0.00	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Oecetis	0.11	0.00	0.00	0.00	0.00	0.22	0.00	0.00	0.00	0.00	0.00	0.00
Lepidostoma	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pycnopsyche	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Marilia	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chimarra	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.67	0.00	0.44	1.44
Polycentropus	0.22	0.00	0.00	0.00	0.00	0.11	0.00	0.22	2.00	15.00	6.78	1.78
Psychomyia	3.00	1.56	0.33	0.56	0.22	1.11	1.44	1.22	0.00	0.00	0.00	0.00